HUMANS IN AN ANIMAL'S WORLD – HOW NON-HUMAN ANIMALS PERCEIVE AND INTERACT WITH HUMANS

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HUMANS IN AN ANIMAL'S WORLD – HOW NON-HUMAN ANIMALS PERCEIVE AND INTERACT WITH HUMANS

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Editorial: Humans in an Animal's World—How Non-human Animals Perceive and Interact With Humans

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Editorial on the Research Topic

Humans in an Animal's World—How Non-human Animals Perceive and Interact With Humans

Whilst humans undisputedly shape and transform most of earth's habitats, the number of animals (captive and wild) living on this planet far outnumbers that of humans. Humans, therefore, inevitably interact with different animals in a variety of contexts: we keep them for companionship, farm them for their products, use them for biomedical research, house them in zoos and sanctuaries, and interact with animals in the wild. How humans engage in these interactions has been extensively debated in areas such as ethics, sociology, and psychology. Given the rise of animal welfare concerns over the last decades, but also our growing interest in understanding the minds of non-human animals, there is now a strong demand to shift from a rather traditional anthropocentric view and focus on how animals themselves perceive and interact with humans in this variety of contexts. Over a range of fields, such as psychology, ethology and animal welfare science, questions on how non-human animals acquire knowledge about humans, how this knowledge is generalised and how it can spread socially are of increasing relevance to mediating conflicts arising from human-animal interactions across different settings (Bensky et al., 2013; Nawroth et al., 2019). This is the focus of this *Frontiers* Research Topic.

This Research Topic comprises 18 articles, including state-of-the-art empirical work as well as review articles concerning the role of humans in the sensory and cognitive world of non-human animals, either in captivity or in the wild. It provides discussions on the applied implementation of these findings (e.g., for conservation attempts or farmed animal husbandry management) and considerations of future interdisciplinary approaches and applications.

COMPANION ANIMALS

The Research Topic attracted many papers examining the cognitive and perceptual abilities of companion animals. This is no surprise given their popularity and immersion in our everyday lives. Dogs, for example, have shared a long journey with humans (Davis and Valla, 1978) and, throughout the domestication process, their communicative abilities to interact with humans have been profoundly affected. In the past, most of the research effort in this area was directed toward humans' understanding of dog behaviours, whereas a new trend emerged in which the focal point is to explore what dogs understand about human behaviours.

The relationship that humans have with their pet dogs is often quite intense, leading to a strong bond with the owner, caregiver, or extended family, including children. Benz-Schwarzburg et al. discuss the nature and ethical dimension of these bonds in the light of current scientific knowledge on the social skills of dogs. The focal point of their review considers human-dog interactions from the perspective of the dog, with the ultimate goal to inform human actions and identify responsibility toward their "best friend." Koyasu et al. reviewed the communication between humans and dogs and humans and cats. Although both species followed different domestication trajectories, both dogs and cats are able to communicate non-verbally with humans. The authors specifically focus on their gazing behaviour which is an important signal for humans, describe the communicative function of dogs' and cats' eye-gaze behaviour with humans, and present a research-based approach to multimodal interactions between dogs/cats and humans.

Interactions initiated by dogs toward humans are a crucial part in the human-dog interplay. For example, the expression of so-called "Puppy Dog Eyes" (i.e., raising of the eye brow) has been suggested to be sensitive to the attentive stance of humans and might thus imply a possible communicative function. However, Bremhorst et al. showed that this expression was more often shown in non-social, rather than social contexts–thus challenging its communicative function, suggesting an association with eye movements as an alternative explanation for its expression. Dogs also often look back to humans when they are confronted with a difficult problem they perceive as unsolvable. Some claim that this might be an indication of decreased problem-oriented behaviour, whilst others interpret this as a stronger motivation to interact with humans in general. To find out whether specific training, such as actively helping people as assistance and therapy dogs, increases problem-oriented behaviour, Carballo et al. compared the behaviour of dogs with different training experiences. They showed that training, and specifically training to help people, led to increased problem-oriented behaviour, and in turn to less human-directed behaviour in an unsolvable task.

The ability of dogs and other companion animals to interact and communicate with humans might also affect therapeutic contexts that cover both humans and companion animals. Grandgeorge et al. explored the pattern of visual attention during dog-child and cat-child interactions in children with typical development and in children suffering from autism spectrum disorders (ASD). While dogs displayed more gazes, cats showed glances, which could be considered more subtle, toward humans. Children with ASD preferentially directed their visual attention toward their pet cat, but the amount of visual attention toward pet cats and pet dogs was similar for the children with typical development. The authors proposed that ASD children perceived their cats' repeated glances less invasively and more comfortably than those of their dogs. This might likely increase the chances for ADS children to develop a bond with their pet cat compared to their pet dogs. Wanser et al. provided evidence that dogs with a secure attachment, measured by the Secure Base Test (Ainsworth et al., 1978) within the context of an Animal Assisted Intervention, have the potential to change the overall attachment style between a family dog and a child to a more secure attachment. For example, dogs with a strong attachment to the parents developed also a more secure attachment to the family's child during the intervention.

Globally, free-ranging dogs constitute the majority of domesticated dogs under direct humans' supervision (Hughes and Macdonald, 2013; Lord et al., 2013) and in some parts of the world the presence of stray dogs living close to urbanised areas presents a challenge because of potential conflicts with the local community. Bhattacharjee and Bhadra examined intraspecific (dog-dog) and interspecific (dog-human) interactions in twelve groups of free ranging dogs living in intermediate and high level areas of human activity, using social network analysis. The analysis revealed that the frequency of interspecific interactions was higher than intraspecific interactions, regardless of the urbanised living condition; humans were the main initiators of positive and negative interactions with the stray dogs. A better understanding of the interactions between stray dogs and humans can thus help to address the concerns generated by stray dogs living in urbanised areas.

Many of the communicative capacities of companion animals toward humans have been proposed to be affected by domestication. In particular, the selection for tameness has been proposed as the primary mechanism of domestication and has also been associated with changes in autonomic nervous system regulation. Jean-Joseph et al. aimed to test dogs and wolves in different activity contexts, either alone, with a human or with a conspecific. Although the authors found context-specific differences between dogs and wolves, e.g., dogs were more relaxed than wolves when at rest and close to a familiar human, no general differences between the two groups emerged suggesting that the impact of selection for tameness on the modulation of the autonomic nervous system is more complex than previously thought.

FARMED ANIMALS

The relationship between humans and farmed animals is under special scrutiny. Farmed animals are kept for production purposes, and economic incentives can often be detrimental to a good human-animal relationship, subsequently leading to diminished animal welfare in general. Although a good human-animal relationship cannot alone ensure good welfare to farm animals, it is a crucial aspect to enhancing their quality of life. Rault et al. review the mechanisms underlying this relationship and particularly highlight the need for reliable indicators for this relationship as assessing the quality of human-animal interactions can be challenging. Crucially, the authors also offer perspectives on how to refine those indicators.

In the relationship between farmed animals and humans, tactile perception, such as gentle stroking, plays a crucial role in decreasing stress, and fearfulness (Hemsworth, 2003; Tallet et al., 2014). Lange et al. refined this approach by investigating whether the perception of human voices, either live or via recordings, during these interactions could affect cows' emotional experience. Their findings suggest that live talking was pleasurable to the animals and had a stronger relaxing effect than voice recordings. Specific details of routine management may also have an impact on the relationship between farmed animals and humans. Aigueperse and Vasseur showed that provision of an outdoor exercise area can affect cows' reactivity toward humans. The authors found seasonal differences of this effect, which they linked to different handling styles over the seasons. That means that the way cows are handled during these events provides opportunities to facilitate future handling.

Beyond being perceived as the individuals that handle animals, humans might also provide a form of enrichment to animals with their mere presence. Villain et al. followed-up on this idea and investigated whether the response of pigs to an inanimate manipulable object and a familiar human differs. After a brief period of isolation, pigs were reunited with either the object or the human. Only the reunion with the human led to the production of positive shorter grunts, usually associated with positive situations, leading the authors to suggest that positive pseudo-social interactions with a human could help to enrich pigs' environment.

More subtle cues from humans, such as gaze direction, can also be perceived by domestic animals. Although previous studies on gaze following were primarily conducted on primates and canids, there has been a recent trend to test more uncommon taxa, including ungulates, in order to identify the evolutionary pressures leading to the emergence of gaze following skills. Schaffer et al. provided experimental evidence of gaze following skills in domestic, but also non-domestic ungulates, highlighting that selection pressures caused by domestication might not be necessary to follow human gaze.

Interactions with humans can also have a profound effect on physiological parameters of farmed animals. Scopa et al. presented a technical study assessing the cardiac activity of horses when they interact with humans. The horses were more relaxed when being physically touched by a familiar handler, as compared to unfamiliar humans. Interactions between humans and farmed animals are almost always not neutral–so these situations can have a strong positive, but also negative impact at the physiological and behavioural level. Studies on interactions between humans and farmed animals may therefore provide practical suggestions on how humans should interact and manage such animals.

WILD ANIMALS

One aspect of human-animal interactions that has received relatively less attention so far are interactions of non-domestic animals with humans, for example in the wild or in a zoo setting. These animals occupy important niches in anthropogenic environments, and future research should focus on how human activity and behaviour may affect their welfare and how to solve conflicts of this cohabitation (especially in animals living in the wild).

Anthropogenic activity has profoundly changed ecosystems and often brought humans and wild animals into close proximity, and occasionally conflict. Therefore, skills such as recognising humans could be particularly advantageous for wild animals as they might enable them to access resources or avoid potentially negative consequences. Goumas et al. review how wild animals modulate their responses toward humans by also describing the most likely cognitive processes involved. In addition, they also discuss how certain cognitive abilities might be under indirect human selection and argue about its potential impact on the wild population. They conclude that future research should aim to better understand these dynamics and inform adequate conservation policies and wildlife management.

Blum et al. investigated the ability to differentiate between humans in captive ravens. In their study, common ravens quickly distinguished between a dangerous human (carrying a dead raven) vs. a non-threatening human. The ravens were still responding to the potentially dangerous human after 4 years without any further associations. Considering that ravens exploit human resources but do not live in highly urbanised areas, they represent a valuable model species to investigate which cognitive mechanisms are involved in individual human recognition. Some wild animals, such as elephants, have a long history of living alongside humans, although they were never domesticated. This context provides an interesting opportunity to test animals for socio-cognitive skills that have largely been investigated in domestic animals, such as dogs (Kaminski and Nitzschner, 2013). Here, Jim et al. investigated whether Asian elephants can form a reputation about humans using direct or indirect experience (e.g., eavesdropping) of human interactions. Their results suggest that when elephants can choose between a cooperative and a non-cooperative human they choose indifferently and the authors discuss potential issues linked with the sample size and methodological details. In particular, they suggest taking species-specific sensory-perceptual abilities into account (Plotnik et al., 2014), especially when the tasks involve interactions with other species.

In a zoo setting, visitors can affect the behaviour of captive wild animals. This so-called "visitor effect" has received scientific attention for the potentially negative impact it can have on animals kept in zoos. However, quite often other factors that are related to visitor activity might lead to an overestimation of the impact of visitors *per se*. In this context, Rose et al. studied the behaviour of hornbills in a zoo setting and found no general visitor effect. The authors here show the necessity to integrate climatic conditions, the sex of the animal and the number of visitors on the behavioural parameters analysed to gain a more complete picture on how visitors might impact on the welfare of zoo animals.

In conclusion, the contributions to this Research Topic expand our understanding of how animals in different contexts and with different life histories perceive and interact with humans, raising new possibilities for mitigating problems where the interests of humans and animals are in conflict with each other.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Assistance and Therapy Dogs Are Better Problem Solvers Than Both Trained and Untrained Family Dogs

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When faced with unsolvable or difficult situations dogs use different behavioral strategies. If they are motivated to obtain rewards, they either try to solve the problem on their own or tend to interact with a human partner. Based on the observation that in problem situations less successful and less perseverant dogs look more at the humans' face, some authors claim that the use of social strategies is detrimental to attempting an independent solution in dogs. Training may have an effect on dogs' problem-solving performance. We compared the behavior of (1) untrained, (2) trained for recreational purposes, and (3) working dogs: assistance and therapy dogs living in families ($N = 90$). During the task, dogs had to manipulate an apparatus with food pellets hidden inside. We measured the behaviors oriented toward the apparatus and behaviors directed at the owner/experimenter, and ran a principal component analysis. All measures loaded in one factor representing the use of the social strategy over a more problem-oriented strategy. Untrained dogs obtained the highest social strategy scores, followed by dogs trained for recreational purposes, and assistance and therapy dogs had the lowest scores. We conclude that assistance and therapy dogs' specific training and working experience (i.e., to actively help people) favors their independent and more successful problem-solving performance. General training (mainly obedience and agility in this study) also increases problem-oriented behavior.

Keywords: human-animal interaction, canine-cognition, persistence, gazing, unsolvable task, working dogs

INTRODUCTION

Problem-solving behaviors involve a diverse set of cognitive processes, such as perception, learning, memory and decision making, among others (1, 2).

Several studies have focused on dogs' problem-solving abilities using a wide variety of tasks (e.g., puzzle boxes in Frank and Frank (3) and Marshall-Pescini et al. (4); unsolvable task in Miklósi et al. (5); string pulling in Osthaus et al. (6); interactive dog toy in Shimabukuro et al. (7). Different kinds of tasks require different skills, thus allowing the thorough study of the diverse strategies that dogs use to solve problems [see e.g., Polgár et al. (8)]. While some studies focus on the manipulation of the physical environment, others analyse social strategies, including communicative interactions. With regard to the latter, dogs' gazing behavior has received the most attention. One frequently used protocol to assess dogs' communicative intents toward people is the so-called unsolvable task. In this situation, dogs try to obtain a reward from an apparatus that cannot be opened. When faced with this problem, most dogs tend to gaze at their owners, which can be interpreted as a referential request for assistance by the human partner [e.g., Miklósi et al. (5), for a review see Cavalli et al. (9)].

Dogs' selection for socio-cognitive abilities during the domestication process might have had a detrimental effect on their physical cognition (3). This hypothesis has been supported by several comparative studies in which dogs privileged the use of social strategies such as gazing to the human face, while wolves spent more time manipulating an apparatus and were thus more successful in solving the problem (10, 11). However, other authors have highlighted that this discrepancy in the performance of the two species may not be (only) due to differences in their ability to solve physical problems, but other factors, such as motivation and persistence (12–14), and vague definitions (15). Persistence is a reliable predictor of problem-solving ability, and might be linked to trial and error learning strategies (16). In this regard, persistence has been operationally defined as the time spent interacting with an apparatus (17). Accordingly, those individuals that persist longer in their problem-solving attempts are more likely to solve a problem than those that give up earlier [e.g., (16)].

Several other factors appear to influence dogs' problem-solving abilities, including their relationship with humans (18), their living conditions (19, 20), and their breed. For example, compared to Siberian huskies, border collies looked more at the owner in an unsolvable problem situation (21), and herding dogs tended to look more at the person than working and mastiff like dog breeds when confronted with a puzzle box (22). However, herding dogs did not interact more with the apparatus than other breed groups in this study, and when taking into consideration both breed and training experience, training had a major influence on dogs' orientation to the apparatus (22).

In line with this, many studies have focused on the role of training experience. This is of particular relevance, considering the importance of training in working dogs' performance and the increased number of tasks in which dogs participate nowadays. For instance, Marshall-Pescini et al. (4) tested the performance of untrained family dogs and highly trained family dogs that participated in different activities (i.e., agility, schutzhund, retrieving, search and rescue, freestyle performances). All dogs were exposed to a commercial feeding box which could be opened by pressing a paw pad or nosing the lid. While untrained dogs spent significantly more time looking at either the experimenter or their owner; trained dogs interacted significantly longer with the apparatus and were more successful in opening it. Marshall-Pescini et al. (22) observed similar results using the same apparatus, as dogs with training experience (i.e., agility, police, search and rescue, and man-trailing) were more successful in the task and looked less to people than untrained dogs. It is important to note that in both of the aforementioned studies trained dogs' groups were heterogeneous given that the subjects differed in the types of training they received and their everyday experiences. While some dogs were trained working dogs, others were trained for recreational or sporting purposes such as agility. Thus, to disentangle the relative effects of training for recreational purposes and for specific work, we aimed to compare the performance of dogs trained for assistance and therapy work with family dogs which had been trained for recreational purposes (see subjects' details). Assistance and therapy dogs differed from trained family dogs in the purpose of their training, their everyday tasks and in the methods of training.

Range et al. (23) carried out a similar experiment, using a wooden box with a handle which could be opened by pushing it down with the mouth or a paw. In line with previous results, trained dogs (i.e., agility and search and rescue) spent more time interacting with the apparatus and were able to open it significantly more often than untrained ones (23). On the contrary, Brubaker and Udell (24) found no significant differences between search and rescue dogs and untrained family dogs in gazing or persistence in a similar task. However, significantly more search and rescue dogs opened the container when they received encouragement (24). The divergence between these studies may be related to differences in the training the dogs from each sample had received [i.e., agility and rescue dogs in Range et al. (23); only rescue dogs in Brubaker and Udell (24)]. Furthermore, the encouragement in Brubaker and Udell (24) may have also influenced the results and this difference in the protocols hinders a straightforward comparison. All in all, results regarding the effects of training on dogs' problem-solving skills and strategies are contradicting. This could be due to differences in the protocols and tasks used, samples, the dogs' breed, and the training received as discussed above.

Professional working dogs represent a special group of dogs which, unlike family dogs, are specifically trained to regularly perform a specific activity such as detection of substances, search and rescue or helping disabled people, among others (25). Importantly, working dogs face a variety of cognitive challenges during their training and working activities which may influence their behavior and performance during cognitive tests. Even more, as different working roles require different sets of skills, it would be expected that working dogs vary in their performance during such tasks according to the specific activities they carry out (26). In line with this, it must be taken into account that there are variations in the goals of training, the methods employed for it and the frequency in which those abilities need to be performed, which add to the expected variability among working dogs as a whole. Thus, it is important to assess dogs with different training and working experiences to further understand how these aspects influence dogs' problem-solving skills.

In this study we focused on two types of working dogs: assistance and therapy dogs. Assistance dogs are individually trained to perform tasks for the benefit of their owner with a disability affecting everyday life situations (27). Therapy dogs participate with their owners in planned, goal-oriented therapeutic interventions directed by providers of health and human service (28). Both types of working dogs need to be sensitive to their owners' wishes, but at the same time they have to be independent in order to solve problems on their own and flexibly adjust to new scenarios.

Gácsi et al. (29) studied the interactions between assistance dogs and their owners during a carrying task. They observed joint attention during different parts of the task as well as the use of both verbal and non-verbal communication to guide the dogs' actions. In the case of a task that was impossible to perform, they observed that assistance dogs did not give up easily and were very persistent before they showed communicative signals directed at the owner (29). The results suggest that assistance dogs are not only persistent, but also able to switch between different strategies, such as communicating with the owner, if they failed in independent problem-solving.

Thus, in this study we aimed to compare the problem-solving performance of dogs with different levels of training and working experience. To this end, we tested three groups of dogs in a problem-solving task; untrained family dogs, family dogs trained for specific tasks (e.g., obedience, agility, herding), and working assistance and therapy dogs. For the sake of simplicity, we will refer to dogs working in assistance and therapy as "working dogs." We expected working dogs to perform better at independent problem-solving and thus to obtain more food rewards than family pet dogs. Also, we expected untrained family dogs to depend more on their owners and prefer the use of a social strategy such as gazing toward people. In the case of trained family dogs, training experience may increase their independent problem-solving abilities [e.g., (4)]. If this is the case, they should behave similarly to the working dog group. Alternatively, the trainings these dogs had (mainly obedience and agility) may have not prepared them for independent problem-solving, thus their performance may be indistinguishable from that of untrained family dogs.

MATERIALS AND METHODS

Ethical Statement

The procedures comply with national and EU legislation and institutional guidelines and in accordance with the recommendations in the International Society for Applied Ethology guidelines (www.applied-ethology.org). In Hungary, the behavioral observations conducted in this study were not identified as animal experiments by the Hungarian Animal Protection Act ("1998. évi XXVIII. Törvény," 3. §9.), which identifies animal experiments, as this study was non-invasive. The application number of the ethical commission by the Pest County Government Office is PE/EA/2019-5/2017. Each owner filled in a consent form stating that they have been informed of the tests. Our Consent Form was based on the Ethical Codex of Hungarian Psychologists (2004).

Subjects

We tested a total of 90 dogs between 1 and 12 years of age, of different breeds and mixed-breeds (see below). Owners volunteered to participate in the test and were recruited through the Family Dog Project database of Eötvös Loránd University, Budapest, Hungary. All dogs had been living with their owners for at least 6 months before the test. Dogs were assigned to three groups according to their work and training experience. Size, sex, and breed were balanced across groups:

1. *Untrained family dogs* had no certification exams. $N = 30$, 14 males, 16 females, mean age = 4.05, SD ± 2.74, breeds: 1 beagle, 7 border collies, 3 German shepherd dogs, 4 golden retrievers, 3 Labrador retrievers, 1 Maltese, 10 mixed, 1 English cocker spaniel.
2. *Trained family dogs* are dogs trained for recreational purposes. They had 1–4 certification exams (27 obedience, 23 agility, 11 herding, 5 guarding, 9 other: rescue dog, frisbee, dog dancing, K99). $N = 30$, 15 males, 15 females, mean age = 4.66, SD ± 2.67, Breeds: 8 Border Collies, 1 Bouvier, 1 Dobermann, 2 Golden Retrievers, 1 groenendael, 1 kelpie, 1 Labrador retriever, 2 malinois, 8 mixed, 1 mudi, 1 sheltie, 2 Hungarian vizslas, 1 Yorkshire terrier.
3. *Working dogs* worked as certified assistance or therapy dogs. assistance dogs were trained to aid individuals with disabilities by the dogs for human charity (http://kea-net.hu/). Therapy dogs were all certified trained dogs, and lived with their owners at their homes. $N = 30$, 15 males, 15 females, mean age = 4.47, SD ± 3.32, 1 Airdale terrier, 3 border collies, 1 Cavalier King Charles spaniel, 4 golden retrievers, 1 groenendael, 1 Irish setter, 2 Labrador retrievers, 1 Malinois, 8 mixed, 2 standard poodles, 1 English cocker spaniel, 4 Tervuerens, 1 Hungarian vizsla.

Experimental Setup

All dogs had at least 1 h of fasting time before the testing. Dogs were tested in a room unfamiliar to them at the Eötvös University, Department of Ethology. Four cameras in each corner of the room videotaped all testing sessions. The room was 3 × 6 m^2 and there was a drawer where the problem box was stored before the start of the test and a chair for the owner to sit on (**Figure 1**).

Apparatus

As a problem box we used a commercial wooden dog toy (Nina Ottosson® Dog Brick) that comprised a rectangular base with eight holes where treats could be hidden. A sliding wooden brick covered eight holes on both longer sides of the toy, so dogs had to slide the covers toward the middle with their paws or nose in order to get the treats. The bricks could not be lifted. Eight pellets of dry food in the eight holes on both longer sides were used as treats. None of the dogs were familiar with the apparatus prior to the task.

Procedure

At the beginning of the test, the owner sat on a chair holding the dog on leash. The experimenter (female, 22 years old), who was the same for all dogs, took the interactive dog toy out from the drawers, placed it on the ground, and put a pellet of dry food inside each hole. Thus, dogs were able to see the baiting. When she was ready, the experimenter stepped back, the owner released the dog and the testing began. The dog had 2 min to obtain the food pellets from the apparatus. During this period, the owner was allowed to encourage the dog to find the pellets, verbally and by pointing at the apparatus, but we forbade the use of any previously trained or known commands relevant to the task such as "catch" or "nose." The owner

FIGURE 1 | The experimental setup. Written informed consents were obtained from the individuals for the publication of this image.

could not touch the apparatus nor the dog (**Figure 1**). After the 2 min had elapsed, the experimenter put the toy back in the drawer. Dogs were allowed to eat only the food pellets they had recovered.

Behavioral Variables

We measured the duration of the vocalizations using a 0–3 score. We also measured the proportion of time dogs spent wagging their tail and the proportion of time oriented to the apparatus (including manipulating it, as gazing at the apparatus was often immediately followed by manipulation, therefore it would have been difficult to separate the two behaviors). We counted the number of times the dog gazed at the owner/experimenter, because gazing was generally a short event (just a glance) and provided more information than duration. We also counted the number of food pellets eaten after the behavior tests, on the spot. Other behavioral measures were coded from the videos using Solomon Coder (©András Péter). See **Table 1** for details and descriptive statistics.

Statistical Analysis

We analyzed the inter-rater reliability of the variables using two-way random intraclass correlation, looking for absolute agreement between average measures. The inter-rater reliabilities were satisfactory (ICC > 0.741, $N = 10$).

After standardizing the variables, we ran principal component analysis and calculated factor scores. Cronbach alpha (CA) was used for checking the internal consistency of the factor. For investigating differences in the behavioral factor score ("social strategy" score, see below), as a function of group, sex (as fixed factors), and age (as covariate) we applied General Linear Model with Student–Newman–Keuls (SNK) *post-hoc* test, including all main effects and two way interactions. We used backward elimination to obtain the minimum adequate model. SPSS v25 (30) was used for the analyses.

RESULTS

Descriptive statistics of the variables and factor loadings are presented in **Table 1**. Standardized variables loaded on a single factor. The total explained variance of the factor was 51.5%, CA = 0.8. The factor included looking at the owner, looking at the experimenter, tail wagging, and vocalization with positive loadings while orientation toward the apparatus and number of food pellets eaten had negative loadings. We labeled this factor as "social strategy," because high score indicated that the dog uses communicative signals toward the human partners, including gazing, vocalization, tail wagging.

Only group affected the social strategy score [$F_{(2,85)} = 16.477$, $p < 0.001$, partial eta squared = 0.275, **Figure 2**), age or sex had no effect and there were no interactions (all $p > 0.05$). According to the SNK *post-hoc* tests, all groups differed from each other (alpha = 0.05). Untrained dogs obtained the highest social strategy scores, trained dogs had lower scores, followed by working dogs.

TABLE 1 | Descriptive statistics of the measured raw variables and factor loadings of the standardized variables.

Behavioral variables	Min	Max	Mean	SD	Factor loading
Duration of vocalization [score 1–3: (score 0: no vocalization, 1: 1–5 s, 2: 5–10 s, 3: >10 s)]					0.47
Untrained	0	3	0	1	
Trained	0	3	1	1	
Working	0	1	0	0	
Number of food pellets eaten (*n*)					–0.75
Untrained	0	4	0	1	
Trained	0	5	1	1	
Working	0	8	3	3	
Duration of orientation toward the apparatus (including manipulation, %)					–0.84
Untrained	3	90	35	25	
Trained	7	99	55	29	
Working	10	100	72	28	
Duration of tail wagging (%)					0.60
Untrained	0	98	49	35	
Trained	0	97	45	30	
Working	0	100	26	31	
Number of looking at the owner (*n*)					0.87
Untrained	3	32	16	7	
Trained	0	33	12	9	
Working	0	20	7	6	
Number of looking at the experimenter (*n*)					0.71
Untrained	0	22	6	5	
Trained	0	13	5	4	
Working	0	13	4	4	

DISCUSSION

We set out to investigate the problem-solving abilities and related behaviors of dogs with different levels of training and working experience (trained and untrained family dogs as well as working assistance and therapy dogs) in a problem-solving task. Working assistance and therapy dogs displayed a less social and more problem-oriented strategy with a higher success rate than both untrained and trained family dogs. The frequent use of social strategies (i.e., gazing) is correlated with less persistence on the task (i.e., independent manipulation of the apparatus) and consequently with lower success (17). The results are also consistent with prior literature stating that animals persisting more on their problem-solving attempts are more successful in actually solving the task (16).

As it was mentioned in the introduction, the literature is mixed regarding the effects of training on dogs' persistence and gazing behavior during problem-solving tasks. For instance, Marshall-Pescini et al. (4, 22) found differences in trained dogs' gazing and persistence patterns, but other authors did not find these differences (18, 24, 31). Results regarding working dogs' abilities should be taken with caution, as dogs from different studies vary in the type and amount of training they have received. For example, dogs in Marshall-Pescini et al. (22) were trained for different purposes (agility, police, search and rescue, and man-trailing), while Brubaker and Udell (24) tested search and rescue dogs, D'Aniello et al. (31) focused on water rescue dogs, and in Topál et al. (18) dogs were trained for basic obedience. A possible explanation is that specific training and working experience confounded the results. We have tried to independently assess (1) the effect of training for recreational purposes as dogs in our trained family group were trained for different hobby activities, mainly obedience and agility, and (2) the effect of specific training, as working dogs were trained as assistance and therapy dogs. Therefore, the type and methods of training could be an important aspect to take into account in future studies. Most probably the broad category "trained vs. untrained" is not precise enough to unravel the effect of training on problem-solving behaviors. Furthermore, working dogs may vary in their independence levels according to the context in which they work. For instance, water rescue dogs did not differ from pet dogs in their interaction with the apparatus during an unsolvable task, but they directed their first gaze significantly more often toward the owner and spent more time gazing at people than untrained pet dogs (31). Water rescue dogs are rewarded for looking at the handler during their training, and during their service they have to remain inactive for a long time in the vicinity of their owners in order not to cause any disturbance, and they take initiatives only upon command. These specific requirements probably affect their performance during problem-solving tasks.

A direct antecedent in the literature is the study of Mongillo et al. (32) who measured dogs' attention toward the owner in untrained family dogs, agility trained dogs, and assisted intervention animals. They assessed the number of gazes and the amount of time dogs spent watching their owner in a baseline condition where the owner walked alone in a room, and in a selective attention test where the owner's movements were mirrored by an experimenter. During the baseline phase, agility dogs shifted their gaze frequently toward the owner and were also the ones who spent the lesser amount of time looking at their owners, while assistance dogs gazed longer. In addition, assistance dogs gazed longer at their owners during the selective attention test. These results support the idea that different training and everyday activities may modify dogs' attentional patterns. Contrary to our results, Mongillo et al. (32) found that dogs participating in animal assisted interventions were the most attentive to their owners. This apparent contradiction could be due to the differences in the task. Unlike Mongillo et al. (32), we presented dogs with a problem-solving situation, in which dogs had to manipulate an apparatus to access a reward. In this latter scenario we observed that working dogs (which include dogs participating in animal assisted interventions) displayed less social strategies than the other group of dogs. Assistant and therapy dogs have to be attentive to their owners' needs but once they understand them or receive a specific command, they should be independent to succeed in their tasks. This interpretation is also supported by the fact that agility dogs in Mongillo et al. (32) shifted their gaze toward the owner more frequently than

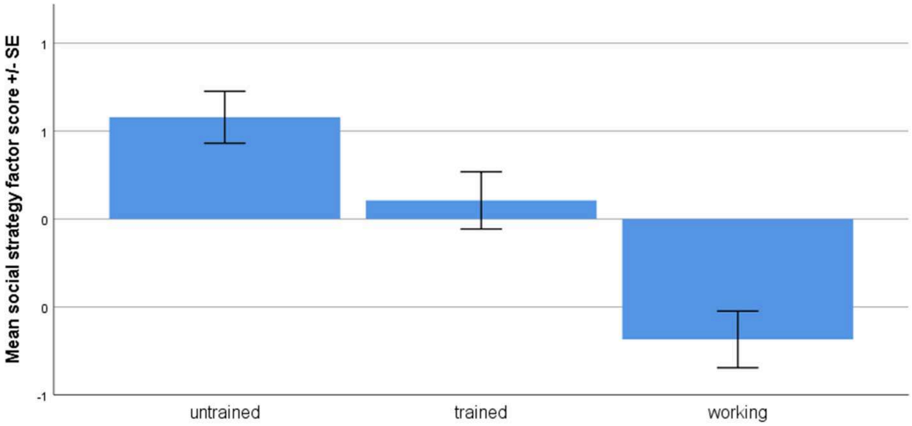

FIGURE 2 | Social strategy factor scores of the three dog groups.

family dogs which is an important feature in the agility sport, but they do not need to solve novel problems independently during it. In our study trained family dogs (which include agility dogs) differed in the use of social strategies from untrained pet dogs. Thus, training for specific purposes may yield different patterns of social behavior depending on the context, emphasizing the plasticity and adaptability of dogs' behavior.

Importantly, according to the SNK *post-hoc* tests, trained family dogs had lower social strategy scores than untrained family dogs. Possibly, trained dogs were more used to facing novel situations and they could have generalized their training experience to this situation as well. It is possible that during training sessions dogs have to persevere and try different behaviors before getting the reward and that the contextual cues of the testing scenario trigger some of those responses. Indirect evidence supporting this idea comes from studies indicating that dogs are able to generalize and learn to follow novel and complex communicative signals faster when they have previously received a brief training phase with a simpler communicative cue (33, 34).

Nevertheless, training for recreational purposes did not seem to be enough for dogs to reach the effectiveness of working assistance and therapy dogs, as the latter were more successful problem solvers and had lower scores in the use of the social strategies component. This result suggests that dogs' everyday experience is an uttermost important aspect to take into account when assessing their skills in a problem-solving situation. There are at least two possible, non-exclusive, explanations for this difference. First, it is possible that working assistance and therapy dogs were more comfortable in the presence of strangers and in novel situations given that they usually accompany their owners to a variety of places. Second, it is possible that dogs that have successfully accomplished the training as assistance or therapy dogs had pre-existing characteristics that distinguished them from other dogs. For instance, it has been shown that personality traits such as boldness are related with the successful training of working dogs (35). We propose that these two explanations are complementary, because it is possible that those dogs that became working dogs were encouraged during their everyday activities to behave in a more independent manner. Owners were allowed to encourage their dogs during the task, verbally or pointing to the apparatus, but without using commands or touch. Interestingly, Udell (11) reported that dogs, who were encouraged, spent more time in contact and looking at the puzzle box, but they were not significantly more successful in solving the task. Similarly, in Brubaker and Udell (24) encouraged family dogs interacted more with the apparatus but their performance was not significantly better. Conversely, encouragement did improve the performance of dogs trained for search and rescue (24). Given that in the present study we did not systematically manipulate the quantity and quality of the encouragement, we cannot derive unambiguous conclusions regarding this aspect. Udell's (11) results suggest that the use of encouragement and verbal instructions modulates problem-solving behavior, but their particular effects could depend on the context as well as working and training experience (11). In this regard, it is also possible that dogs react differently to verbal commands. Working dogs are trained to respond to a command by performing a specific action. For example, if the owner points to a particular object and asks the dog to do something with it, trained working dogs will manipulate the object instead of looking at the owner, while untrained pet dogs may be uncertain about what to do and will gaze at the owner in search for further clues [similarly to young dogs in Miklósi et al. (5)]. Furthermore, not only the type of commands given by the owner affects dogs' performance, but also the bond between them. Topál et al. (18) compared the performance of dogs categorized according to their relationship with the owners. "Companion dogs" were defined as dogs living indoors as a member of the family and "working dogs" were kept outside the house as a guard or for some other purpose. In a simple manipulative task dogs had to manipulate an apparatus in order to get the reward while the owner could encourage them to retrieve the food. Companion dogs gazed more at the owner, started to manipulate the apparatus later and also retrieved less food than working dogs. The authors also found that obedience training did not affect dogs' performance or gazing patterns to their owners. These results are in line with our findings about the similar gazing patterns between trained and untrained family dogs.

One limitation of the study is that the dogs' characteristics before training were unknown. As it occurs in many studies assessing the effect of training on dogs' cognitive skills, the lack of a baseline measurement before training makes it impossible to guarantee that dogs were not selected for such work based on their pre-existing characteristics such as an increased persistence. Another limitation of these kind of studies is that training methods may differ between specific trainers and yield different results on dogs' problem-solving strategy. Thus, in future research, specific types and methods of previous training should also be taken into account when assessing dogs' problem-solving skills.

Summing up, we have shown that working assistance and therapy dogs were more independent problem solvers compared to both trained and untrained family dogs, who privileged a more social strategy. Thus, although assistance and therapy dogs need to show highly developed social understanding in their interactions with the owner, their special training and work may have increased their persistence and independent problem-solving skills. However, obtaining training certificates (mainly obedience and agility in this study) also increased the independent problem-solving tendency in our task, suggesting that trained family dogs generalize their training experience of facing novel situations and perseverance for obtaining rewards.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by Pest County Government Office, PE/EA/2019-5/2017. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

EK, ÁM, and MG designed the experiments and collected the data. EK analyzed the data. FC, CC, and EK wrote the first draft. All authors finalized the manuscript. ÁM and EK provided funding.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2020.00164/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Why the "Visitor Effect" Is Complicated. Unraveling Individual Animal, Visitor Number, and Climatic Influences on Behavior, Space Use and Interactions With Keepers—A Case Study on Captive Hornbills

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A "visitor effect" on zoo-housed species has been documented since the 1970s, with research focused on mammals (specifically primates). To broaden our understanding of the "visitor effect" in a non-mammal, we conducted a case study on a pair of hornbills, recording behavior and aviary use alongside of visitor and keeper presence. Temperature and humidity were significant predictors of visitor number, and temperature was a better predictor of hornbill exhibit use than visitor presence. Behavior was significantly affected by the presence of keepers and individual variation in behavior was noted too. Visitor number mediated any interest in a keeper by birds: high visitor number decreased a bird's interest in its keeper. Whilst only a case study on a pair of birds, our research shows that any "visitor effect" is heavily influenced by other environmental variables and that different categories of human (i.e., visitor, keeper) affect how zoo animals utilize their environment.

Keywords: *Ceratogymna atrata*, black-casqued hornbill, bird behavior, visitor effect, keeper effect, zoo animal welfare

INTRODUCTION

For most zoo animals, the visitor presence is a normal part of their daily routine. Since the early 1970s, researchers have suggested that this visitor presence may play a role in modifying the behavior of the animals being observed (1, 2). As reviewed by Davey (3) the 'visitor effect' has been described in many early studies as a negative influence on animal behavior, decreasing maintenance behaviors or increasing aggressive interactions. Alternatively, research can also show no observable change in behavior with visitor presence or intensity (4, 5) and in some circumstances, the presence of visitors may be enriching (6), particularly where visitor- animal interaction has a positive outcome (2). For example, gentoo penguins (*Pygoscelis papua*) show increased pool usage and positive increases in behavioral diversity with increasing visitor number (7) and a long-billed corella (*Cacatua tenuirostris*) performed "attention-seeking" behaviors, such as bobbing up and down and dancing on the spot, directed at visitors standing at the bird's enclosure (4).

Considerable interest has also focused on the effect of keeper presence on the behavior of zoo animals (8). As daily providers of resources, the work of a zookeeper may be an enriching feature of the captive environment but, for some species, this human presence within their environment could be negative (9). For many mammals, the human-animal relationship that can develop between an animal and its keeper may be beneficial to the animal's welfare state (6). Experienced keepers are more likely to recognize potentially negative behavioral changes in mammalian charges compared to non-mammalian ones (10), and the increasing recognition of a keeper by the animal reduces the stress of having humans in and around the enclosure (11, 12).

Whilst there is considerable interest in assessing both visitor and keeper effects, studies may be limited. It is often difficult to determine a baseline behavior for a study subject, particularly in zoos that are open to the public every day (3). Evaluation of research findings may be further complicated by limited prior information on the species and researchers may find it tricky to determine which behaviors are indicative of changes in welfare state (13). Methods to measure the visitor effect include assessment of visitor number, noise and behavior (2)—different taxa will vary in their responses to these factors, creating difficulties when designing repeatable research projects (14).

Much of the existing visitor effects literature has a mammalian focus, with primates dominating (2, 15). Zoos house a multitude of non-primate, non-mammalian taxa that may also be affected by visitors and this diversity in zoo-housed taxa means that studies assessing the visitor effect across a wider-range species would be beneficial (3) to inform husbandry practices and welfare assessment.

As such, the aim of this research was to determine any influence of human presence on a representative species of commonly housed zoo bird, a hornbill (Bucerotidae). Species360's Zoological Information Management System (ZIMS) database identifies over 2,600 hornbills housed in global species360-registered institutions as of August 2019 (16). Hornbills remain challenging to breed in captivity (17), and further research would be beneficial to identify the impact of humans on captive hornbill behavior, and thus provide evidence that may help understand any further influences on reproduction. The species focus for this research was the black-casqued hornbill (*Ceratogymna atrata*), a large hornbill from Africa, known for its sophisticated cognitive capabilities (18) with a decreasing wild population trend (19). Wild black-casqued hornbills (hereon referred to as "hornbill") are normally found in pairs (20), but small groups of up to five birds are frequent and congregations of up to 40 individuals have been found on fruiting trees (21). This species feeds on at least 19 species of fruit in the wild and also invertebrates as a supplementary food source (22). Given their flexible social system and diet, this hornbill is a relevant study subject for analyzing the relationship between variable husbandry influences (i.e., human presence), behavior, and welfare as have evolved to cope with a very heterogeneous, widely fluctuating environment. More widely, a general lack of research on captive hornbill behavior, coupled with their poor reproductive success in zoos (23–25) but need for conservation action due to declining wild populations (26, 27), makes study of hornbill behavior and welfare in the zoo of increasing relevance and importance.

MATERIALS AND METHODS

Subjects and Study Design

Data collection took place from 13th to 31st August 19 at Blackpool Zoo, Lancashire, UK and 17 days of observation were conducted in total. A pair of hornbills (both ∼1 year of age) were observed for 90 h. The hornbills were housed with a pair of blue cranes (*Anthropoides paradiseus*); the enclosure included an indoor area measuring ∼3 m^3 (containing feeding and drinking areas, heat lamp and perches) connected to an outdoor exhibit measuring ∼20 m (length) × 8 m (width) and from 8 to 10 m in height. The outdoor section contained various furnishings, such as natural planting and perches (see a schematic illustration of the enclosure in **Supplementary Figure 1**). No interaction between the hornbills and the cranes was noted during the observation period, nor did the hornbills actively seek to avoid the presence of the cranes.

An ethogram (**Table 1**) was developed using previous research from Kozlowski et al. (17). Each day consisted of 6-h of observation: 10:00 to 12:00; 12:20 to 14:20; and 15:00 to 17:00. Each hour of each observation period was considered a separate sampling event for data analysis (see "Data analysis"). This timeframe enabled capture of the varying numbers of visitors across each day; from when visitors first started arriving at the Zoo through to when the vast majority leave. Due to the short period of observation, no data were collected during periods of time when visitors were not within the Zoo. State behaviors ($n = 90$ records per bird) were recorded using instantaneous focal sampling at 1-min intervals (28), as was the location of each bird (indoor or outdoor exhibit) within the enclosure. A total of 10,740 min of behavioral data were collected per bird.

To explain potential behavioral changes associated with the number of visitors, the observer started recording the location of each bird from the third day onwards ($n = 80$ records/bird). Visitor number was counted each minute and the mean value was used to determine groupings into high, medium or low visitor number (high = mean of 13+ visitors/minute; medium = mean of 7–13/minute; low = mean of 1–7/minute) for each hour. Categorization was based how busy the viewing areas of the enclosure appeared to the observer and how much of the enclosure was visible to the observer when different numbers of people were gathered around. Visitors could look into the viewing window of the indoor enclosure but the viewing area was small; the inside house kept darker and more secluded for the hornbills, who could perch away from, and higher than, the main window so had the choice to be in or out of view (see **Supplementary Figure 2**). Hornbills had *ad lib* access to and from the indoor enclosure during the duration of the study. The presence or absence of keepers was also recorded each minute, for each observation period. Visitor and keeper presence were recorded in areas visible to the birds (within or around their enclosure), approximate distance of up to 20 meters away from enclosure out the front and visible side (near outdoor area of enclosure) and 10 meters out from back (other side of enclosure

TABLE 1 | Ethogram of captive black-casqued hornbill state behaviors.

Behavior	Description
Preening	Using beak to manipulate feathers anywhere on the body. Normally carried out whilst perching and lasting longer than 10 s.
Allopreening	Using beak to manipulate the feathers of another individual bird, anywhere on its body.
Foraging	Picking up food items and/or water using the beak, head is tilted back or jolted upwards and slightly backwards, throwing items toward the back of the mouth. Includes swallowing of food items. Some vocalization may be made.
Standing	Terrestrial. No movement along ground, however minimal head and wing movement may occur. No direct interest toward anything specific. Some vocalization may be made.
Perching	Sat/stood on a branch or any structure off the ground. No movement along or around structure, however minimal head and wing movement may occur. Some vocalization may be made.
Sunbathing	Perched or stood, with wings spread open or drooping down slightly, may be leant out and showing back to heat source (likely to occur near or under a heat source or in sunny weather).
Locomotion	Ariel or terrestrial. Flying using wings. Or putting one foot in front of the other either along the ground or along a branch, to walk or hop.
Inactive	Perched or sat motionless with head resting on back of body, no interaction to other individuals or its surroundings.
Out of Sight	The animals are not visible to observer, and possibly most visitors outside the enclosure.

by the indoor area). The mean (±SD) number of visitors was 8.8 (±0.12), with the minimum being 1 person and the maximum being 51 people. For all periods of data collection, the observer was considered a visitor.

Local weather conditions (rain, cloudy, sunshine), temperature and humidity were recorded for the start of each observation hour using the Met Office website https://www.metoffice.gov.uk. For the overall study period, the mean (±SD) temperature was 17.01°C (±0.14) and humidity was 80.24% (± 0.90). The most common weather condition was cloudy.

Data Analysis

Data were analyzed in R studio v. 1.2.19 (29). To analyze the potential effect of visitors, local weather conditions (including temperature and humidity), keeper presence, and individual bird ID on state behaviors and on time spent outside compared to inside, mixed effects models with date blocked as a random factor to account for the repeated measurements were run using the "lmertest" package in R (30). The "MuMIn" package (31) was used to calculate r^2 values for each model run.

To determine any effect of temperature, humidity, and weather (cloudy, raining, or sunny) on daily visitor numbers at the hornbill enclosure, a general linear model was run. Anecdotally, zoo visitors are known to gather around an enclosure when they see a keeper working inside, and therefore Spearman's rho correlation was run on the time spent by a keeper in the enclosure and the mean number of visitors at the enclosure for that hour of observation. The same correlation was run to check any relationship between the temperature and humidity for each observation hour.

Based on descriptive analysis (**Figure 1**), minutes spent preening (as a comfort behavior), out of sight (as a potential indicator of stress based on how the birds could hide themselves away in different areas around the inside and outside enclosure), inactive (as measure of limited behavioral diversity, i.e., birds spending the majority of their time inactive may not be performing a full daily time-activity budget) and foraging (as an exploratory behavior) per observation period per day were included as dependent variables. Out of sight (i.e., being away from visitors) and inactivity are noted in Nimon and Dalziel (4) as behavioral outcomes of different levels of visitor effect on another species of socially and cognitively complex bird, hence their inclusion here. Temperature was included in the modeling of preening, foraging or inactivity and visitor number, and for the time birds out of sight. The interaction between visitors and temperature was also included, as well-individual bird ID, and finally date (as the random factor).

To see whether time of day influenced these three behaviors and time out of sight, in conjunction with the visitor and temperature interaction, time of the observation was coded (morning from 10:00 to 12:00; noon from 12:00 to 13:50; afternoon from 13:50 to 17:00) and included in a further mixed effects model, again with date blocked as a random factor. Time codes were based on discussion between the three authors as to the most practical, biologically-relevant, and optimal for capturing change in visitor/keeper presence way of categorizing when observation occurred.

Output is presented from the anova (model name) function in RStudio. *Post-hoc* testing using the "lsmeans" and "pbkrtest" packages (32, 33) was run for behaviors were time code showed a significant relationship to change in activity. To unpick any impact of when keepers might be in with the birds during different times of the day, and hence changing bird activity, the mean number of minutes for each time category was calculated to see at what times of the day keepers were in with the hornbills for longest.

Interest from each bird (measured as the number of minutes that a bird looked in the direction of or moved toward the keeper or visitor) was included as the dependent variable in a mixed effects model to determine any influence of keeper presence (time in minutes at or in the enclosure), visitor number and individual bird ID, again with date blocked as a random factor.

Significant outputs from the generalized linear models run are provided in the results section with estimate ± standard deviation, r^2 value, degrees of freedom, t value and *P*-value at the 5% level. For relevant non-significant results, *P*-values are given.

RESULTS

State Behaviors

A time activity budget was developed to show the behavior of both the male and female hornbill under low, medium and high visitor numbers (**Figure 1**).

To investigate the relationship between visitors and weather, linear models were run to identify any significant predictors

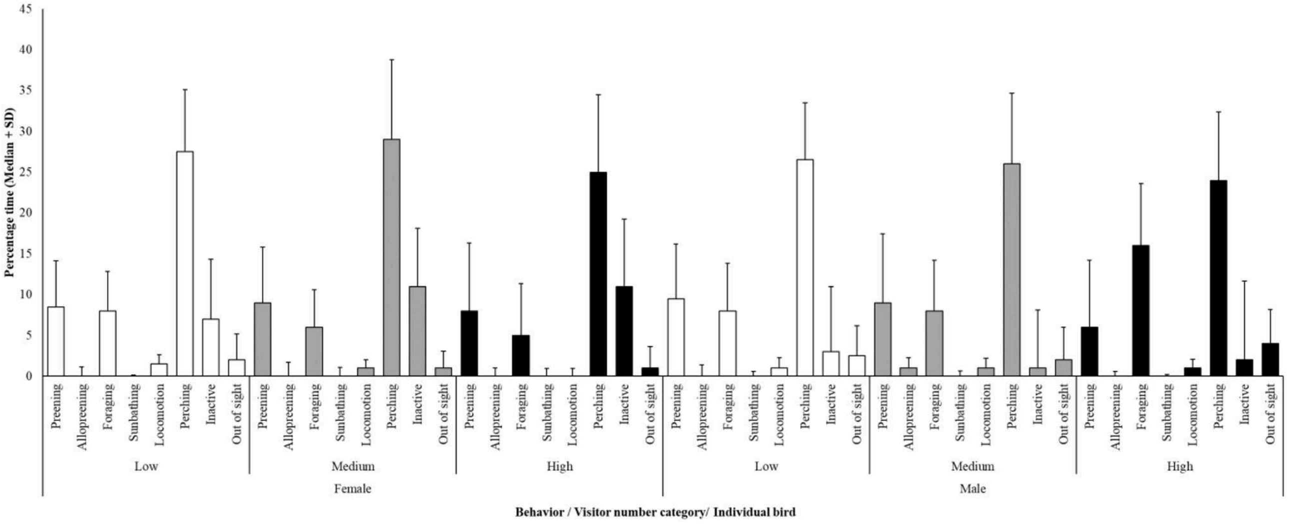

FIGURE 1 | Average (± standard deviation) time-activity budget for the female and male hornbill against different categories of visitor number. White bars, low visitor number; Gray bars, medium visitor number; Black bars, high visitor number. Perching is the most commonly observed behavior and time spent perching is consistent between these two individuals and across visitor number categories.

of increased visitors to the zoo. There is no effect of weather condition on visitor number ($P = 0.731$) but there is a significant influence of temperature and humidity. Significantly more visitors are present on hotter days (estimate = 1.25 ± 0.259; $df = 175$; t-value= 4.83; $P < 0.001$) and significantly fewer on more humid days (estimate = -0.198 ± 0.039; $df = 175$; t-value = -2.78; $P = 0.006$). Temperature increase showed a positive correlation with humidity ($n = 26$; $r = 0.585$; $P = 0.002$) and this was the justification for including temperature in the modeling of bird behavior / time out of sight and visitor number plus other relevant interactions (see "data analysis" section).

There are no significant effects on preening behavior for either hornbill ($P = 0.956$). There is an individual difference for time being out of sight (estimate = 1.044 ± 0.416; $r^2 = 37\%$; $df = 159.6$; t-value= 2.51; $P = 0.013$), which is significantly higher in the male bird than the female bird in this case. All other predictors of time spent out-of-sight are non-significant. The same difference is seen for foraging, with the male spending more time foraging than the female (estimate = 3.31 ± 0.814; $r^2 = 28\%$; $df = 157.9$; t-value= 4.09; $P < 0.001$). Again, there is no significant effect of visitors, temperature or the interaction between them on time spent foraging. Finally, the individual bird also significantly predicts, with the female hornbill spending more time inactive than the male (estimate = -4.82 ± 1.09; $r^2 = 28\%$; $df = 159.6$; t-value = -4.44; $P < 0.001$). All other potential predictors of inactivity were non-significant.

Time of day (category) does not significantly predict when hornbills would be preening [$F_{(2,167.9)} = 0.969$; $r^2 = 19\%$; $P = 0.381$], foraging [$F_{(2,166.9)} = 0.163$; $r^2 = 28\%$; $P = 0.849$], or out-of-sight [$F_{(2,165.01)} = 2.24$; $r^2 = 38\%$; $P = 0.109$] but it does predict when these birds are likely to be inactive [$F_{(2,168.3)} = 3.2$; $r^2 = 29\%$; $P = 0.04$]. Birds are more likely to be inactive in the afternoon compared to in the morning (estimate = 3.91 ± 1.58; $df = 169$; t-ratio = 2.48; $P = 0.04$), irrespective of temperature*visitor number (estimate = 0.101 ± 0.06; $df = 172.8$; t-value = 1.71; $P = 0.09$). Keepers were likely to visit the hornbill enclosure more frequently in the morning but stay for shorter times ($N = 30$; mean = 1.93 ± 0.14) compared to afternoon visits that were less frequent but longer in duration ($N = 18$; mean = 4.11 ± 1.13).

Enclosure Occupancy

Modeling predictors of time spent outside for both hornbills including individual bird ID, visitor number, temperature, interest in visitors from the birds, and the relationship visitor number* temperature shows an overall significant fit (estimate = 135.6 ± 30.23; $r^2 = 51\%$; $df = 98.34$; t-value = 4.473; $P < 0.001$; **Figure 2**). The effect of visitor number on time spent inside or outside is significant- an increasing number of visitors suggests less time inside for the birds (estimate = -7.18 ± 2.63; $df = 151.84$; t-value = -2.73; $P = 0.007$). However, as the relationship between visitor number and temperature is also significant, the cause of the hornbills being increasingly outside with higher visitor numbers is explained by higher temperatures (estimate = 0.313 ± 0.150; $df = 151.24$; t-value = 2.09; $P = 0.039$). There is no individual bird difference for time spent inside or outside ($P = 0.189$). **Figure 2** illustrates the relationship between enclosure occupancy and temperature.

Keeper and Visitor Presence and Hornbill Interest

For 71% of all occurrences ($n = 90$) no keeper was present within or near the enclosure (**Figure 3**). Using these remaining data where a keeper was present, the birds' degree of interest in the keeper and in the visitors (based on minutes of observation from the hornbills) was analyzed. As keeper presence and visitor

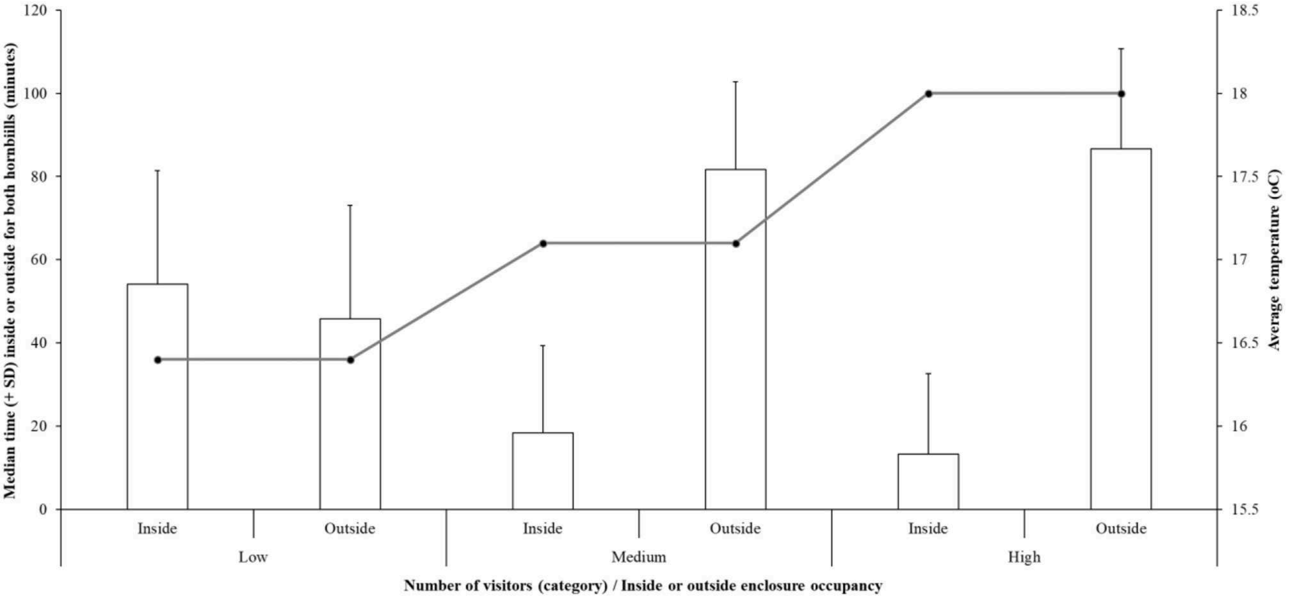

FIGURE 2 | The time (for both birds combined) spent inside or outside (median number of minutes ± standard deviation) compared to the three categories of visitor number and average temperature for these visitor categories.

number correlated ($n = 26$; $r = 0.442$; $P = 0.024$) the interaction between keeper presence*visitor number on bird interest in both was included in the model.

There is a significant interaction between the presence of the keeper in or near the enclosure and an increasing interest from the bird (estimate = 0.864 ± 0.99; $r^2 = 85\%$; $df = 9.43$; t-value= 8.64; $P < 0.001$). There is no significant effect of bird interest in visitors ($P = 0.419$), visitor number ($P = 0.395$) and individual bird ID ($P = 0.223$). The interaction between visitor number*keeper presence is a significant factor (estimate $= -0.026 \pm 0.01$; $df = 27.44$; t-value $= -3.403$; $P = 0.19$) on the hornbill's interest in the keeper, suggesting that birds become less interested in the keeper as visitor number grows (**Figure 3**).

When running this model for the bird's interest in visitors there is no effect of keeper presence ($P = 0.937$) and the interaction between visitor number*keeper presence also becomes non-significant ($P = 0.546$). Individual bird is significant (estimate $= -1.76 \pm 0.783$; $r^2 = 50\%$; $df = 36.71$; t-value $= -2.25$; $P = 0.03$) with the female bird spending more time interested in visitors than the male (overall minutes of interest per observation period from the female 3.9 ± 0.34 and for the male 2.8 ± 0.26).

DISCUSSION

Overall, we identified no direct "visitor effect" on the behavior of this pair of hornbills and our results support recent findings, using a mammalian species (the ring-tailed lemur, *Lemur catta*) that the visitor effect may be overestimated (34) if other behavioral influences are not fully considered. For these hornbills, several other variables, such as the individual characteristics of the birds themselves, had greater influences on their behavior.

Behavior

Significant differences in time-activity budgets were identified for these hornbills, with the male spending longer foraging and the female more time inactive. The female hornbill was less likely to be out-of-sight compared to the male. Time of day significantly predicted increases in activity, with the hornbills being more active in the morning compared to the afternoon. Time (minutes) that a keeper spent in the enclosure may be influencing activity, with the shorter, but more frequent morning visitors causing more interest from the birds in the daily husbandry routine. However, temporal changes in inactivity could be explained by the natural ecology of these birds- wild hornbills are known to use vocalization to organize social groups to move from roosting sites to foraging sites in the early morning (25). Expanding data collection into the earlier morning and later evening to capture husbandry influences on the birds (e.g., the provision of fresh food) would help unpick this complicated, multilayered relationship.

These hornbills rarely engaged in behaviors suggestive of pair bonding (e.g., allopreening), potentially because these birds are relatively young and recent arrivals to this Zoo. The female also showed significantly more interest in visitors and this may be related to the bird's inactivity and/or personality, as a bolder or less nervous individual may be less motivated to move away from visitors. Personality is known to affect how highly-cognitive species engage with human interactions in and around their enclosure (35, 36), so further assessment of bird personality traits alongside of state behavior data could be useful in explaining reactions to visitors and keepers. Well-established hornbill pairs

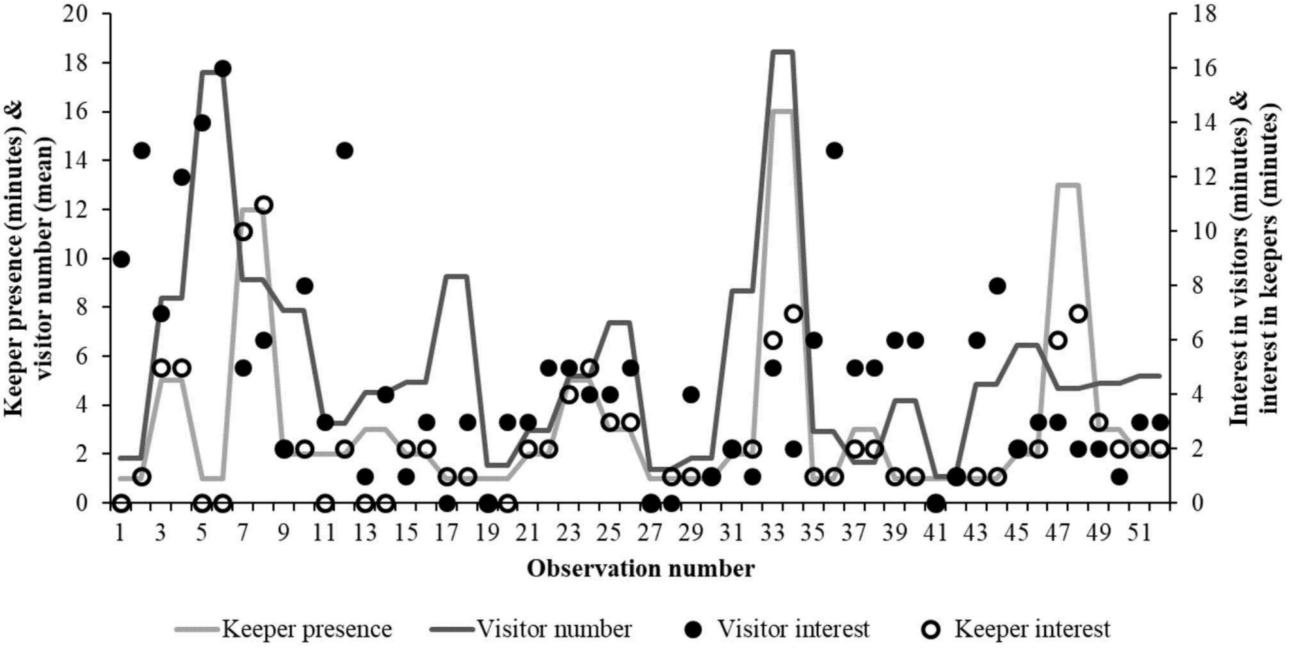

FIGURE 3 | The relationship between the bird's interest in keepers and the visitor number (around the enclosure) and keeper time within and around the enclosure. As visitor number increases, the bird's interest in the keeper is shorter. The lack of relationship between visitor interest and visitor number suggest a role for the keeper in this human-animal relationship.

spend more time involved in social behavior directed at their partner (17, 20). The immaturity of these study birds may have resulted in more interest in their surroundings compared to in each other.

There were no other significant impacts on hornbill time-activity budgets, aside from individual difference. Behaviors selected for further analysis—foraging and preening—are often used as welfare indicators for captive birds (37), and based on the results presented here, there are no marked changes in the performance of these behaviors under different conditions that we measured (i.e., low, moderate, and high visitor number). Perching, as the commonest behavior observed, was also consistent between conditions; measurement of where birds are perching (height and distance to or from visitors) could help further evaluate this behavior. Wild frugivorous hornbills predominantly forage in the upper and lower canopy (38) so perch height and food placement may influence overall time-activity patterns of captive birds. Large species of frugivorous hornbills are known to be selective in their foraging choices and can spend up to 60 min at a specific fruit source (39). Changes to how food is presented around the enclosure, e.g., multiple locations where birds need to work for a reward (25), may encourage more foraging and exploration time and reduce time spent perching or inactive in large hornbill species in captivity. Black-casqued hornbills are also known to wander extensively across a large feeding range (40), so increased enrichment and abilities for flight in their enclosures may reduce time spent inactive and perching.

Enclosure Occupancy

Enclosure zone use is often linked to welfare assessment for zoo-housed animals, with avoidance of specific zones a potential inference of poorer welfare (41, 42). Our model including individual bird ID, climate and visitor numbers, explained 51% of the observed zone use for the hornbills. Initial analysis suggested that higher visitor numbers appeared to be associated with increased use of the outdoor exhibit. However, this relationship is less assured when climatic variables are included in the model. Consequently, consideration of all factors that influence animal behavior and enclosure usage is required when attempting to quantify any "visitor effect," as other more fundamental reasons may produce a more robust, biologically-relevant explanation, of the individual's behavior.

This enclosure may have provided sufficient species-appropriate areas for these hornbills to have the choice to move away from visitors, therefore no avoidance behaviors (i.e., decreased enclosure zone occupancy or repeated, perch to perch hopping) were performed. Choice to be on or off show is known to correlate with the performance of behaviors that indicate improved welfare (43), so the lack of visitor effect may in part be due to the settled nature of the two hornbills in their exhibit and their ability to "cope" with visitor numbers. Further evaluation of enclosure usage alongside of time-activity patterns is required to fully understand the suitability of this aviary for these hornbills, however.

The Visitor and Keeper Effect

Our results show that "visitor effect" is more complicated than it may appear, and the presence of visitors alone may be not the complete causative factor in changing the behaviors of these hornbills. Our results support Goodenough et al. (34), who show that weather and changes in time of day are stronger influences on zoo animal behavior than visitors themselves, and those of de Azevedo et al. (44) who show no visitor effect on behavior in another common zoo bird, the greater rhea (*Rhea americana*). Consequently, research into animal behavior, including visitors as an independent variable must factor in temporal and climatic changes. Further analysis of visitor behavior may help to identify the presence of possible visitor effects on animal welfare; for example via assessment of changes to the soundscape around the enclosure caused by visitors and any accompanying animal response (14, 45). Observation of the visitors by the author of this paper who conducted data collection (JS) noted that as visitor number increased, the immediate vicinity was generally noisier but overall, the hornbill's enclosure was in a "quieter part" of the Zoo. Personal observation also noted that visitors did not generally stop talking at the enclosure and in small to moderate groups, normal conservational noise levels were apparent. Visitors were also noted as walking past without stopping at the hornbills as if the enclosure had not been recognized.

There was a clear relationship between the minutes that a keeper was present around the birds and the birds' interest in the keeper. However, when visitor numbers were higher, the hornbills reduced their focus on keepers. This relationship is further complicated by the fact that there was no significant relationship between visitor number and visitor interest from birds. These birds maybe habituated to visitors (because visitors provide no benefit or threat), but that their presence remains a distraction when coupled with other stimuli. Distraction of bird behavior by human actions is noted in other literature in relation to noise levels and approach to nesting colonies in the wild from groups of tourists, e.g., negative impacts on hoatzin, *Opisthocomus hoazin*, activity (46) and other authors investigating "distraction" effects caused by human activities suggest that species can habituate over time (47), therefore such mechanisms may be at play in the captive environment too. If keepers spend less time in the enclosure when visitor numbers are higher, this may also impact on the bird's attention that is directed toward them. Measurement of the influence of visitor presence on keeper duties and time spent in an enclosure would be a useful follow up to this research. The positive correlation between visitor number and the keeper being present is also worthy of further investigation. Anecdotally, zoo visitors are drawn to an enclosure when a keeper is present as "something interesting might be happening" and therefore further adding to the dynamics of the interaction between the animal on display, its keeper(s) and how it perceives the influence of visitors.

As providers of resources, but also invaders of space, zookeepers may be a source of both enrichment and stress (6). Unlike visitors, keepers can enter an exhibit daily and therefore habituation by the animals may be difficult (8). Anticipatory behaviors, performed based on the timing of specific aspects of husbandry (e.g., feeding), can be indicative of underlying motivational states (48) and their performance may also impact on the keeper-animal relationship (i.e., more interest in the keeper if a positive outcome is expected). Husbandry variables influence the visitor effect on the behavior of mammalian species (49); there is considerable scope for determining such husbandry impacts on non-mammalian behavior under different visitor conditions to fully appreciate animal responses to the zoo environment.

Future Directions

This is a case study on a pair of hornbills of one species at one zoological institution, therefore wide-scale application of these results is limited. We have only one measure of individual bird characteristic (sex) and further study onto the effects of animal personality on the potential of the visitor effect is recommended, this animal personality can predict differences in responses to zoo visitors in captive mammals (36). Multiple measurement of behavior across days when visitor number is low would provide stronger evidence for the link between environmental conditions and outside enclosure usage, and how visitor presence influences this. A proximal cause of behavior change in these birds may be visitor presence and without measure of temperature effects independent of visitor presence, the relationship remains complicated. Specialized species of birds (i.e., those evolved for particular environmental conditions) are noted as having especially aversive reactions to visitors when prevailing environmental conditions are not optimal (50). As is noted in mammalian research, fully pinpointing behavior change caused by visitor presence and then inferring welfare state from it remains a challenge (51). With taxa such as birds, where outward signs of personality and behavioral expression can be harder to judge than in mammals, the visitor-behavior-enclosure usage-welfare relationship could be even more challenging to unpick. Extending this research to other populations of this hornbill in other zoos would enable further analysis of husbandry and enclosure variables on behavior patterns and aviary usage. It is possible that indirect visitor effects may be more prevalent than current research suggests. In order to extend this question further, researchers should consider the following:

- Investigate animal behavior across a range of time periods and seasons to fully capture the influence of weather conditions on behavior and zone occupancy, and their relationship with visitor numbers.
- As zoos move away from single-species aviaries toward larger, mixed-species and/or walk-through exhibits (52) knowledge of any potential visitor effect on enclosure usage would be relevant to animal husbandry.
- Comparing remote (e.g., trail camera) and in-person data collection would enable evaluation of any observer

effect on animal-to-visitor, animal-to-keeper, and animal-to-observer interaction.

CONCLUSION

Our study identified no impact of visitors on hornbill behavior or enclosure use. Visitor number positively correlated with temperature and so temperature should be factored into future visitor studies to avoid overestimation of any visitor effect. Individual hornbill characteristic (e.g., sex) was a significant predictor of behaviors such as foraging and inactivity, whereas visitor and keeper presence and weather conditions were not. When more visitors were present at their exhibit, hornbills spent less time showing interest in their keepers, suggesting more complexity to the keeper-animal relationship in certain conditions. Further research into both visitor and observer effects, across a range of hornbill species, over different seasons, and in different exhibit styles is recommended.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

This animal study was reviewed and approved by Sparsholt College Hampshire Ethics Committee.

AUTHOR CONTRIBUTIONS

JS: data collection and methods. PR: writing and data analysis. JB: editing and fact checking plus supervision of data collection.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2020.00236/full#supplementary-material

Supplementary Figure 1 | Schematic plan (not to scale) of the hornbill enclosure at Blackpool Zoo.

Supplementary Figure 2 | Hornbill indoor housing with visitor viewing area (photo credit: J. Scales).

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Humans Dominate the Social Interaction Networks of Urban Free-Ranging Dogs in India

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Research on human-animal interaction has skyrocketed in the last decade. Rapid urbanization has led scientists to investigate its impact on several species living in the vicinity of humans. Domesticated dogs (*Canis lupus familiaris*) are one such species that interact with humans and are also called man's best friend. However, when it comes to the free-ranging population of dogs, interactions become quite complicated. Unfortunately, studies regarding free-ranging dog–human interactions are limited even though the majority of the world's dog population is free-ranging. In this study, we observed twelve groups of free-ranging dogs in their natural habitat, the streets. We quantified their interactions at the intra (dog–dog) and interspecific (dog–human) levels. The study areas were divided into two zones, namely – intermediate and high flux, based on human activity or movement. Social network analysis revealed higher instances of interspecific than intraspecific interactions, irrespective of the human flux zones. Humans, in significantly higher occasions, initiated both positive and negative behaviors in comparison to dogs. Our findings conclude that humans are a crucial part of the interaction network of Indian free-ranging dogs.

Keywords: human-animal interaction, dog–human interaction, free-ranging dogs, human flux, social network analysis

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INTRODUCTION

Domesticated dogs (*Canis lupus familiaris*) have a long and rather intricate co-evolutionary relationship with humans (Vilà et al., 1997; Savolainen et al., 2002; Thalmann et al., 2013; Frantz et al., 2016). Dogs and humans share very warm social relationships, driven primarily by the abilities of dogs to communicate with humans, much more than any other species. Domestication has been proposed to be a critical factor in facilitating dogs' ability to read human cues and gestures (Hare et al., 2002; Hare and Tomasello, 2005). Numerous studies have also pointed out the role of ontogeny, through shared experiences with humans, in developing such capabilities in dogs (Wynne et al., 2008; Udell, 2015). Consequently, researchers have concluded that such high degree of socio-cognitive skills is probably the result of the dual influence of evolutionary history and ontogenic experience of individuals through socialization (Gácsi et al., 2009; Lampe et al., 2017). More recent studies have postulated that these skills of dogs could also be attributed to their "differential behavior" (Range et al., 2019) leading to increased conflict-avoidance and "hypersociability" (VonHoldt et al., 2017) accounting for their greater sociability toward humans. Undoubtedly, these socio-cognitive skills have enabled dogs' successful co-existence with humans.

Despite significant advancement in the understanding of the evolution of the dog–human relationship, little is understood of how the majority of the world's dog population interact with humans. Nearly 80% of the world's dog population is represented by free-ranging dogs, found in the global south (Hughes and Macdonald, 2013; Lord et al., 2013). They occur as natural breeding populations living without direct human supervision (Serpell, 1996; Bonanni et al., 2011; Bonanni and Cafazzo, 2014). Free-ranging dogs are also genetically more diverse and geographically widespread than purebred dogs (Shannon et al., 2015). Free-ranging dogs are scavengers, depending primarily on human-generated resources for subsistence (MacDonald and Carr, 2016). Unlike other urban-adapted animals that maintain a wary distance from humans (Rodewald and Shustack, 2008; Carrete and Tella, 2011; Samia et al., 2017), free-ranging dogs have been shown to interact with humans regularly. Therefore, exploring the various facets of free-ranging dog–human interactions can help us understand the evolution of the dog–human relationship better.

In India, free-ranging dogs have been living for many centuries as a natural population (Debroy, 2008; Shannon et al., 2015). They are present in every possible human habitat, from forest fringes to metropolitan cities (Vanak and Gompper, 2009; Gompper, 2013; Bhattacharjee et al., 2020a). The relationship of these dogs with humans is quite complex and multidirectional, ranging from very negative to very positive. For example, free-ranging dogs are potential reservoirs of various zoonotic diseases, including rabies, posing a threat to humans and the wildlife (Belsare et al., 2014; Gompper, 2015; Home et al., 2017). Moreover, they scatter garbage, defecate in open spaces, and bark at night, thus being considered as a menace. Humans, on the other hand, influence the behavioral dynamics of free-ranging dogs too. These dogs are often beaten, threatened and even killed by humans (Paul et al., 2016). Still, they choose dens close to human habitats (Sen Majumder et al., 2016) and are cared for by some humans as well. Also, there are several groups across the country, mostly in large cities, working toward the welfare of free-ranging dogs (Totton et al., 2010; Demirbas et al., 2017). These dogs not only scavenge among refuse but use active begging from humans as a strategy for foraging (Bhadra et al., 2016). A recent pan-India survey revealed a significant variation in the human perception of free-ranging dogs across different human habitats (Bhattacharjee et al., 2020a). Hence, investigating the direct interactions between free-ranging dogs and humans can provide us with significant mitigation measures on the conflict of the two species.

Though free-ranging dogs are not owned and do not undergo training or habituation to particular humans, the urban habitats provide an environment for varied interactions between humans and free-ranging dogs in India. A series of studies have investigated the socio-cognitive skills of free-ranging dogs, emphasizing their relationship with humans. For example, their ability to follow simple and complex human pointing gestures (Bhattacharjee et al., 2017a, 2019). Additionally, they have been shown to display situation-specific responsiveness to typically used human social cues (Bhattacharjee et al., 2018, 2020b). In urban habitats, free-ranging dogs regularly encounter unfamiliar humans and experience a range of behaviors. A study concluded that these dogs do not establish physical contact with unknown humans in the first place, but, trust-building can happen with repetitive social contact within a short span of time (Bhattacharjee et al., 2017b). In a recent study, we found that the sociability of these dogs is correlated with human flux or movement in a given area (Bhattacharjee et al., 2020a). We concluded that dogs in the intermediate human flux zones, typically represented by urban neighborhoods, are more sociable in comparison to dogs in high human flux zones, represented by areas like railway and bus stations, marketplaces, etc. In the intermediate human flux zones, sociability, thus could probably be a response to higher positive dog–human interaction than the other zones. It is also necessary to understand that we did not quantify the negative interactions and did not have information on the ontogenic experience of the dogs. Therefore, the underlying reasons for such variation in sociability were not assessed; we assume that direct interactions between dogs and humans would be the first step to have some valuable insights.

In this study, we carried out behavioral observations on groups of free-ranging dogs in intermediate and high human flux zones. We recorded their activities in terms of intra-(dog–dog) and interspecific (dog–human) interactions and subjected these to social network analysis (SNA). SNA is a powerful tool which can be used to understand various patterns of interactions among social animals (Wasserman and Faust, 1994). Given their complete dependence on humans for sustenance, we hypothesized that humans are a crucial part of the interaction network of free-ranging dogs in urban environments. As higher flux of humans may result in higher interactions with dogs, we expected to observe a higher frequency of interspecific interactions (both positive and negative) in the high flux zones, as compared to the intermediate ones. However, since the dogs are typically not very active (Sen Majumder et al., 2014b), the data obtained was not large enough to predict the detailed dynamics of intra and interspecific interactions.

MATERIALS AND METHODS

Study Area and Subjects

We conducted the study in different parts of the following two cities – Bengaluru (12°97′16″N and 77°59′46″E), Karnataka and Raiganj (25°63′29″N, 88°13′19″E), West Bengal, India. We used a "zone categorization criterion" (HF: $\geq$ 60; 60 $<$ IF $\geq$ 10) developed earlier by us (Bhattacharjee et al., 2020a) to identify intermediate and high human flux zones. Based on the criterion, we defined high and intermediate flux areas, where human movements were $\geq$60, and $<$60 to $>$10 per minute, respectively. We typically considered crowded areas like market places, bus and railway stations for high, and partial residential areas with shops for intermediate human flux zones. We chose random spots in the areas and stood there for 1 min between 1600 – 1800 h to count the number of people and vehicles that passed by. We repeated the process at least five times to calculate the average human flux in each area. The process was consistent for characterizing the study areas. We randomly selected six dog groups (average group size: 6.5 ± 2.88) in the intermediate and 6 groups (9 ± 4.38) in the high human flux zones (**Supplementary Table S1**). Groups were defined when dogs were either sitting or moving together within a distance of ≤1 m of each other (Sen Majumder et al., 2014a). All the groups were mixed-sex (male-female) groups and distantly located from each other (**Supplementary Figure S1**), without any possibilities of interactions. Observations were carried out between June 2018 to August 2019.

Observations on Dog Groups

We used a mixture of 5-min All Occurrences Sessions (AOS) and 1-min Instantaneous Scan session interspersed by 2-min breaks to carry out focal group sampling of behavior during the study (Altmann, 1974). We recorded the behavioral "events" or interactions between the focal group members and with humans using AOS data. Scan data were obtained to have information on the behavioral "states," not events. For this study, we only used data from AOS, emphasizing interactions. However, for convenience, we have reported the complete method of sampling here. Each group was observed for 24 observation sessions of 2 h duration each, distributed over different days. Each 2-h session thus had 12 AOS, and 12 scans, distributed randomly and pre-prepared sheets (with randomized AOS and Scan timeslots) were used for recording data to minimize observer bias (Gadagkar, 2001). The observations were carried out in different time slots (0700 – 0900 h, 1000 – 1200 h, 1300 – 1500 h, and 1600 – 1800 h), to cover most of the time when humans and dogs are likely to interact on the streets (Sen Majumder et al., 2014a).

Observations were carried out on each of the different timeslots six times, summing up to a total observational period of 48 h for a focal group. However, we pooled the data from the different timeslots for our analyses. None of the groups was observed more than twice (also not on consecutive timeslots) on a particular day. Since we were interested in understanding dog–human interactions, we did not investigate the effects of different seasons like pre-mating, mating, and pup-emergence (Sen Majumder et al., 2014a), which may influence the intraspecific dynamics of dogs. Moreover, 1-year long observation of groups enabled us to capture general information on dogs' interspecific interactions with humans. The observation was done from a certain distance (not less than 15 m) in order to avoid influencing the dogs.

Data Analysis

We noted all the intra (dog–dog) and interspecific (dog–human) behaviors from the AOS and subjected these to SNA and statistical modeling.

(a) Behavior – Intraspecific behaviors were considered when members of a focal dog group interacted among each other. However, differentiation was not done between the types of intraspecific interactions, e.g., agonistic or affiliative. We only counted the number of instances when such interactions occurred. Interspecific behaviors, on the other hand, were defined when members of a focal dog group interacted with humans. Since dog–human interaction was the primary focus, we quantified all possible components of the interactions, including directionality. Dog – human interaction on the streets can be bidirectional, where both humans and dogs can initiate behaviors toward each other. We further subdivided the behaviors into two major categories – positive and negative. We summarized all the interactive behaviors that are typically seen between dogs and humans –

- *Dog – induced positive* – Positive or affiliative behaviors by dogs directed toward humans. Behaviors included any of the following – gazing with tail-wagging, begging while standing or sitting close to humans (≤0.3 m), and licking humans with tail-wagging.
- *Dog – induced negative* – Agonistic behaviors shown toward humans by dogs. It included either of the following behaviors – attacking humans, barking, chasing, snarling, growling, and biting.
- *Human-induced positive* – Affiliative behaviors exhibited toward dogs by humans. It primarily included positive social petting and food provisioning by humans. Positive vocalizations (Bhattacharjee et al., 2017b) from humans were also considered.
- *Human-induced negative* – Negative behaviors showed by humans toward dogs. This included threatening of dogs by various means, beating, and shooing away (Bhattacharjee et al., 2018, 2020b).

(b) Network analysis – SNA was performed to visualize and subsequently analyse the data. Following are the brief details of the network properties used in the analysis –

Network–A total of 12 networks were generated in this study. Every individual dog in a focal group was considered as a node. Additionally, we defined "humans" as nodes in all the networks. It should be noted that the node "human" represented the species, and thus did not have an individual identity. Therefore, each network consisted of $n + 1$ nodes (n = number of dogs in a focal group, and 1 = an additional node denoting all humans that the individuals in the group were seen to interact with). Edge was defined by a line or link between two nodes, illustrating an interaction.

Node strength–Node strength was used to designate the number of edges or weight between two nodes. For example, if node "i" interacted with node "j" 5 times, it would have a strength of five. We calculated the node strength for intra and interspecific interactions separately. Besides, we measured the strength of the positive and negative behaviors induced by dogs and humans toward each other for the interspecific interactions. In this study, all the edges in the networks were directional and weighted. We also used colors to categorize the type of behavior (gray – positive, red – negative) in the graphs. Therefore, directionality (in terms of who induced a behavior), type of behavior, and strength of interactions were measured. In the graphical representations, the higher thickness of the edges represented higher interactions between the corresponding nodes. In order to make the node strength independent of activities, all edge weights were divided by the largest weight observed for each network to generate normalized weights. Also, to address the varying node sizes, we divided the previously adjusted node strength by the corresponding $n + 1$ values. Thus, global scores were obtained, which were used for the analysis.

Degree (In and Out-degree)–Degree of a node was defined by its unique connections to the remaining nodes. In-degree of a node was considered as the number of unique nodes exhibiting any behavior toward it. Similarly, out-degree of a node depicted any behavior originating from it, toward the total number of unique nodes. For example, in a network with six nodes ($N = 6$), node "*i*" can interact with the five ($N – 1$) remaining nodes. Now, if the node "*i*" initiates an interaction or directs behavior toward three unique nodes, it will have an out-degree value of three. On the contrary, if the node "*i*" receives behaviors from four unique nodes, the in-degree value of node "*i*" would be four.

Degree centrality–This defines an individual's structural importance in a network. Degree centrality was calculated by dividing the degree value of a node with the remaining number of nodes in the network. We calculated in and out-degree centrality. Considering the above hypothetical network, "*i*" will have an out-degree centrality [$C^{D}_{\text{Out}}(i)$] value of 0.6 (3/5), and in-degree centrality [$C^{D}_{\text{In}}(i)$] value of 0.8 (4/5).

Network centrality–This is the measurement of centrality for an entire network, estimated using the degree centralities of the nodes. We used an index called Network Centrality Index (NCI^{D}) to analyze network centrality (Bhadra et al., 2009). Since we had directed networks, In-degree centrality (NCI^{D}_{In}) and Out-degree centrality (NCI^{D}_{Out}) indices were used for better understanding of the data. Network centrality indices were calculated in the following way –

$$NCI^{D}_{In} = \sum_{i-1}^{n}[C^{D*}_{\text{In}} - C^{D}_{\text{In}}(i)]/(n-1)\ (n-2)$$

[C^{D*}_{In} = largest observed in-degree value in network N; n = Total number of nodes].

Similarly, NCI^{D}_{Out} was calculated using the following formula

$$NCI^{D}_{Out} = \sum_{i-1}^{n}[C^{D*}_{\text{Out}} - C^{D}_{\text{Out}}(i)]/(n-1)\ (n-2)$$

[C^{D*}_{Out} = largest observed out-degree value in network N; n = Total number of nodes].

Both the NCI^{D}_{In} and NCI^{D}_{Out} values ranged from 0 to 1. A value of 1 indicated a highly centralized network where one of the nodes either initiated all behaviors directed toward others (out-degree) or received all the behaviors from others (in-degree). Therefore these indices provided information on an actor's (node) role in controlling the network.

Average clustering co-efficient–The overall level of clustering or connectedness in a network was measured in addition to network centrality. For example, if a node "*i*" has k_i nodes as neighbors and they are connected, then at most $k_i(k_i - 1)/2$ edges can exist between them (Watts and Strogatz, 1998). Subsequently, the average value was calculated based on the number of nodes in a network. The values ranged from 0 to 1. A higher clustering coefficient value indicated a more connected network (i.e., stronger interactions among the nodes), whereas a lower value denoted a less connected network (weaker interactions).

Additionally, we calculated the small world (SW) character of the networks. Small-world networks are named with the analogy of "small-world phenomenon" (Milgram, 1967). They are characterized by having higher clustering, and a lower average distance between nodes (Watts and Strogatz, 1998) as compared to random and regular (lattice) networks, respectively. SW was calculated by dividing the clustering coefficient by average distance (Watts and Strogatz, 1998; Bhadra et al., 2009). The range of the SW character was 0–1, with higher values indicating more small-world like networks.

Statistics

We carried out a generalized linear model (GLM) analysis to understand the effect of human flux zones on the clustering coefficients of the networks, using a Poisson distribution with a "log" link function. A GLM analysis was performed for investigating the effects of human flux zones (Categorical – high/intermediate), and interaction types (Categorical – intraspecific/interspecific) on the number of such interactions. The number of interactions was normalized using the node size of a network. Thus, it allowed us to carry out the analysis across all the networks. We used a Poisson distribution with a "log" link function. We controlled the model for varying network sizes further by adding node size as a control variable.

In the next step, we conducted another GLM analysis to assess the effects of human flux zones and types of NCI^{D} (Categorical – NCI^{D}_{In}/NCI^{D}_{Out}) on the values of NCI^{D}, using a Poisson distribution with a "log" link function. As discussed earlier, NCI^{D} values were calculated after controlling the different node sizes of the networks. Finally, we investigated the effects of human flux zones (Categorical – high/intermediate), behaviors initiated (Categorical – positive/negative), and initiators (Categorical – dog/human) on the number of interactions using a Poisson distribution with "log" link function. Like earlier, the number of interactions was not absolute values as they were normalized to control for varying node sizes. We also added node size as a control variable in the model.

For all the models, null vs full model comparison was carried out to eliminate Type I error. We first checked the interactive effects of the explanatory variables, in case of no significance, we looked at the individual effects of the predictors. We used the Akaike information criterion (AIC) values (Akaike, 1974) for model selection. We calculated the Δ_i values by subtracting AIC_i (AIC of i'th model) from AIC_{min} (model with minimum AIC). A Δ_i of six was followed (Richards, 2005). Residual diagnostics of the models were done using the "DHARMa" package of R (Hartig, 2020). GLM analyses were conducted using "lme4" package of R (Bates et al., 2015). The effect plots were made using the "effects" package of R (Fox and Hong, 2009). The alpha level was 0.05. All statistical analyses were performed using R Studio (version 1.2.5019) (R Development Core Team, 2015). Social network analysis was done using Cytoscape (version 3.8.0) (Shannon, 2003).

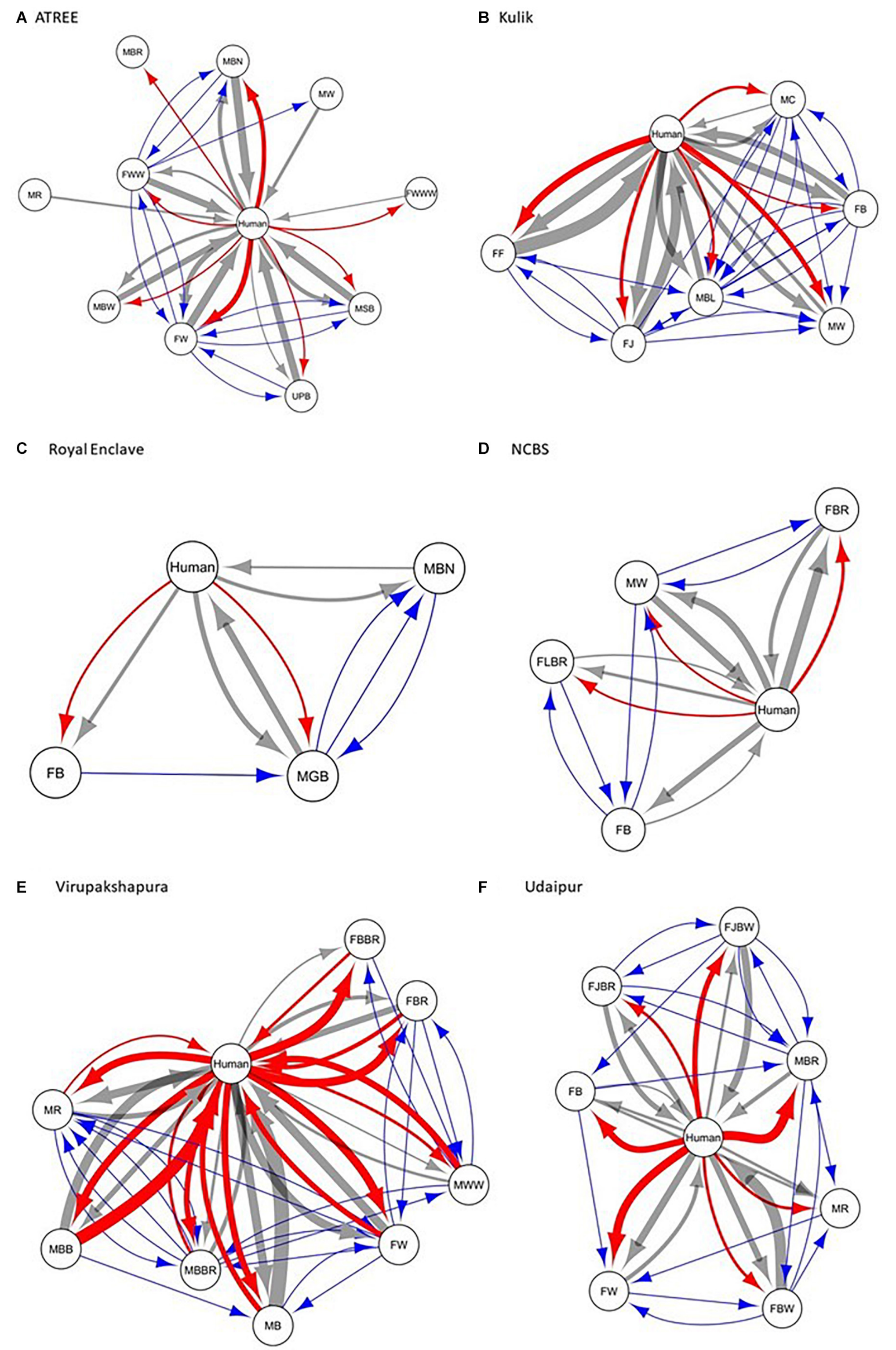

FIGURE 1 | A plot showing the social interactions between dogs and humans in the intermediate human flux zones – **(A)** ATREE, **(B)** Kulik, **(C)** Royal Enclave, **(D)** NCBS, **(E)** Virupakshapura, and **(F)** Udaipur. Circles indicate nodes [dog group members (**Supplementary Table S1a**) and humans] and connecting lines represent edges. Intra and interspecific interactions are represented by different colors: gray – positive interspecific, red – negative interspecific, blue – intraspecific interactions. All the edges are weighted, indicating the strength of interactions – thicker edges represent stronger interactions, whereas thinner edges represent weaker interactions. All the edges are directed, providing information on nodes initiating and receiving such behaviors.

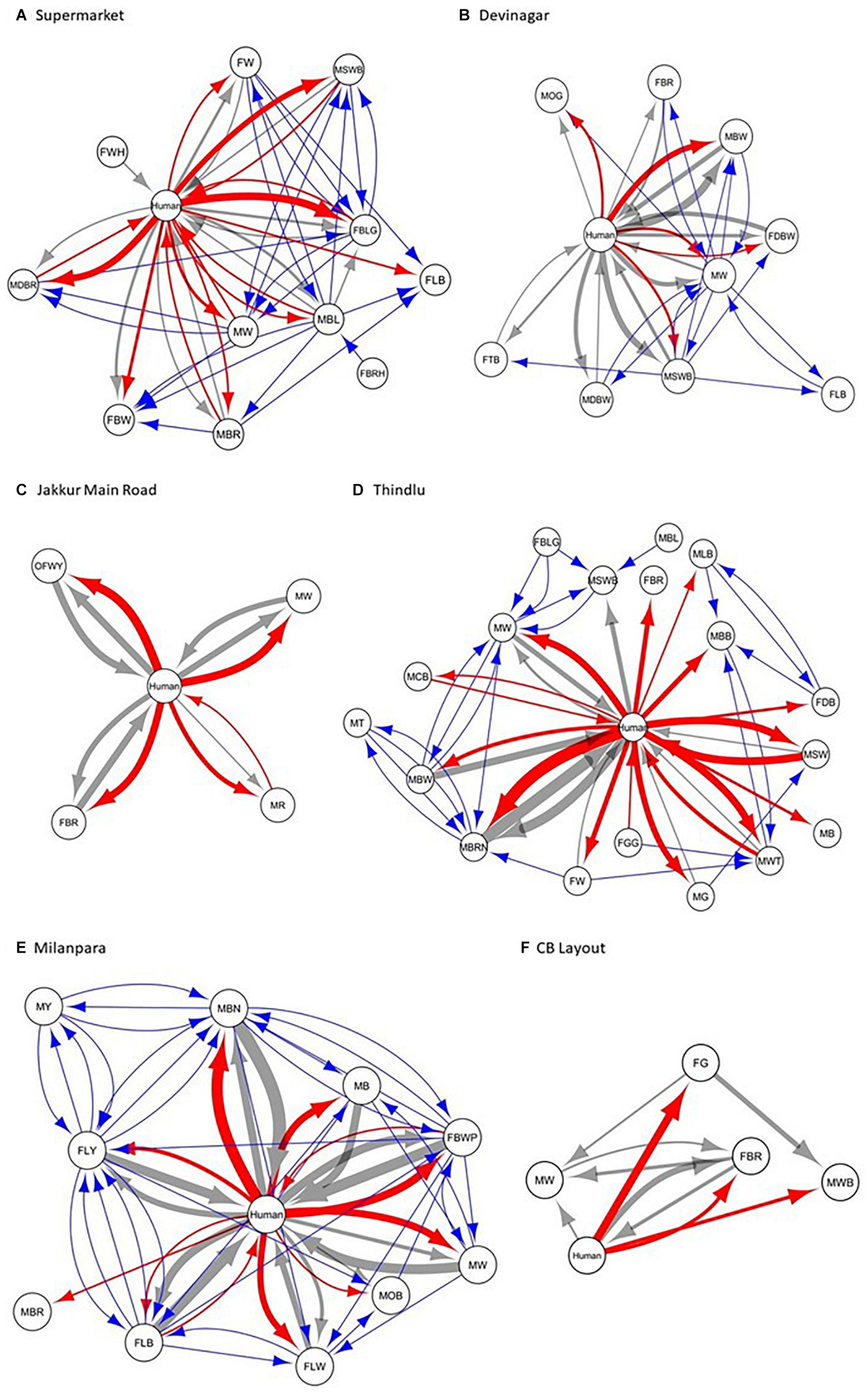

FIGURE 2 | Continued

FIGURE 2 | A plot showing the social interactions between dogs and humans in the high human flux zones – **(A)** Supermarket, **(B)** Devinagar, **(C)** Jakkur Main Road, **(D)** Thindlu, **(E)** Milanpara, and **(F)** CB Layout. Circles indicate nodes [dog group members (**Supplementary Table S1b**) and humans] and connecting lines represent edges. Intra and interspecific interactions are represented by different colors: gray – positive interspecific, red – negative interspecific, blue – intraspecific interactions. All the edges are weighted, indicating the strength of interactions – thicker edges represent stronger interactions, whereas thinner edges represent weaker interactions. All the edges are directed, providing information on nodes initiating and receiving such behaviors.

RESULTS

We constructed the social networks (**Figures 1**, **2**), followed by estimating the network parameters. We summarized the network parameters, including SW and NCI^D in **Tables 1**, **2** for the intermediate and high human flux zones, respectively.

GLM analysis revealed significantly higher connectedness of nodes among the networks in the intermediate human flux zones in comparison to the high human flux zones (**Table 3** and **Figure 3**). The average clustering coefficient was found to be 0.67 ± 0.11 and 0.36 ± 0.30 in the intermediate and high human flux zones, respectively. Therefore, the groups were more connected in terms of intra and interspecific interactions in intermediate human flux zones than the high human flux zones.

We found a significant interaction effect between the two kinds of zones and interaction types predicting the instances of such interactions (**Table 4** and **Figure 4**). Interestingly, we noticed significantly higher instances of interspecific interactions in the intermediate human flux as compared to the high flux zones ($p < 0.001$). Intraspecific interactions were also found to be significantly higher in the intermediate than in the high human flux zones ($p < 0.001$). Therefore, dogs were actively interacting with conspecifics and with humans more in the intermediate as compared to the high human flux zones.

NCI^D values of the networks were found to be predicted by an interactive effect of human flux zones and NCI^D types (**Table 5** and **Figure 5**). $NCI\ ^D_{Out}$ was found to be significantly higher in the high human flux zone than the intermediate zone networks, suggesting higher centrality in terms of initiation of behaviors by one of the nodes. Further investigation revealed that the node 'human' was responsible for initiating behaviors ($NCI\ ^D_{Out} = 0.78 \pm 0.15$) toward dogs, therefore causing increased centrality in the networks.

TABLE 1 | Table summarizing the network parameters of the intermediate human flux zone networks.

Groups (Networks)	Network parameters						
	Nodes	*CL*	*dia*	*d*	*SW*	*NCI* $^D_{In}$	*NCI* $^D_{Out}$
ATREE	11	0.456	3	1.769	0.26	0.74	0.63
Kulik	6	0.717	2	1.333	0.53	0.46	0.43
Royal Enclave	3	0.75	2	1.333	0.56	0.66	0.66
NCBS	4	0.767	2	1.3	0.58	0.5	0.5
Virupakshapura	8	0.7	2	1.542	0.45	0.71	0.69
Udaipur	7	0.630	3	1.536	0.41	0.42	0.61

CL, clustering coefficient; dia, network diameter; d, average path length; SW, small-world value; NCI $^D_{In}$*, in-degree network centrality; NCI* $^D_{Out}$*, out-degree network centrality.*

TABLE 2 | Table summarizing network parameters of the high human flux zone networks.

Groups (Networks)	Network parameters						
	Nodes	*CL*	*dia*	*d*	*SW*	*NCI* $^D_{In}$	*NCI* $^D_{Out}$
Supermarket	12	0.454	3	1.620	0.27	0.54	0.65
Devinagar	7	0.788	3	1.679	0.47	0.55	0.69
Jakkur MR	4	0	2	1.6	0	1	1
Thindlu	15	0.473	5	2.193	0.21	0.51	0.81
Milanpara	10	0.49	3	1.67	0.29	0.38	0.63
CB Layout	4	0.433	3	1.625	0.26	0.5	0.91

CL, clustering coefficient; dia, network diameter; d, average path length; SW, small-world value; NCI $^D_{In}$*, in-degree network centrality; NCI* $^D_{Out}$*, out-degree network centrality.*

TABLE 3 | Generalized linear model showing the effect of human flux zones on the clustering coefficients of the networks.

Fixed effects	Estimate	Std. error	*z*-value	Pr(>|*z*|)
Intercept	3.58352	0.06804	52.667	<2e-16***
Human flux "intermediate"	0.61619	0.08444	7.298	2.93e-13***

****p = 0.*

We found an interactive effect between the type of behavior initiated and initiator, predicting the number of interspecific interactions (**Table 6** and **Figure 6**). Humans were found to initiate both positive ($p < 0.001$) and negative ($p < 0.001$) behaviors in significantly higher instances than the dogs. We did not see any impact of human flux zones.

DISCUSSION

Our findings clearly suggest a central role of humans in the social interaction networks of free-ranging dogs in India. Contrary to our prediction, interspecific interactions were higher in the intermediate than in the high human flux zones. This indicates that human flux alone cannot be predictive of the magnitude of interspecific interactions. It was further corroborated by the higher average network clustering coefficients in the intermediate human flux zones, pointing to higher connectivity within these networks than in the high human flux zones. Dog-initiated behaviors toward humans were, overall, more positive than negative. Additionally, $NCI\ ^D_{Out}$ was close to 0.8 in the high flux zones due to significantly higher levels of human-initiated behavior toward dogs. Humans initiated both positive and negative behaviors comparatively more than the dogs. In other words, humans played a vital role in the dynamics of social interaction networks of these dogs.

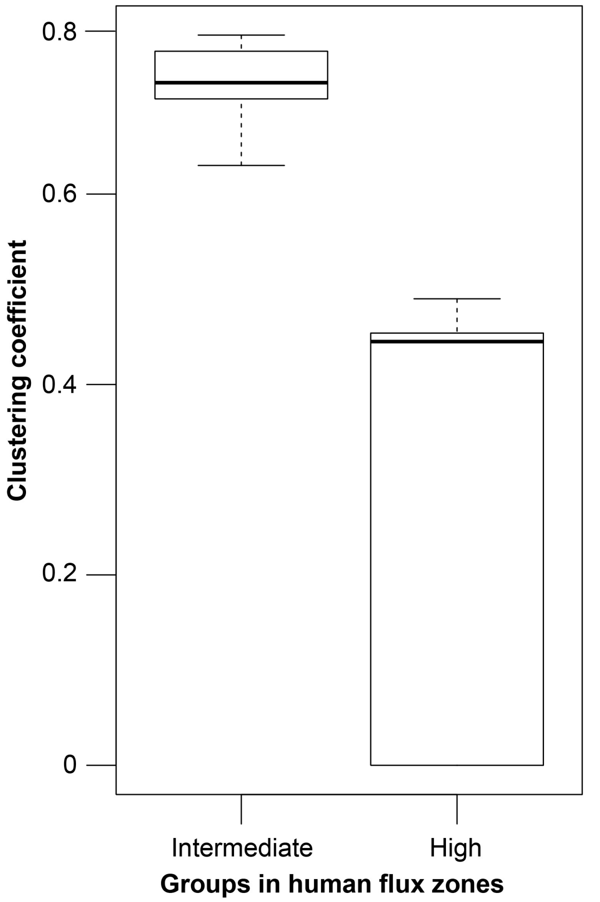

FIGURE 3 | A box and whisker plot showing the network clustering coefficients. Boxes represent the interquartile range, horizontal bars within boxes indicate median values, and whiskers represent the upper range of the data.

TABLE 4 | Generalized linear model showing the interactive effects of human flux zones and interaction types on the number of such interactions.

Fixed effects	Estimate	Std. error	*z*-value	Pr(>| *z*|)
Intercept	5.406298	0.031181	173.38	<2e-16***
Human flux "intermediate"	0.441334	0.02203	20.03	<2e-16***
Type "intraspecific"	−0.363599	0.024513	−14.83	<2e-16***
Intermediate * intraspecific	−0.361752	0.033772	−10.71	<2e-16***

****p = 0.*

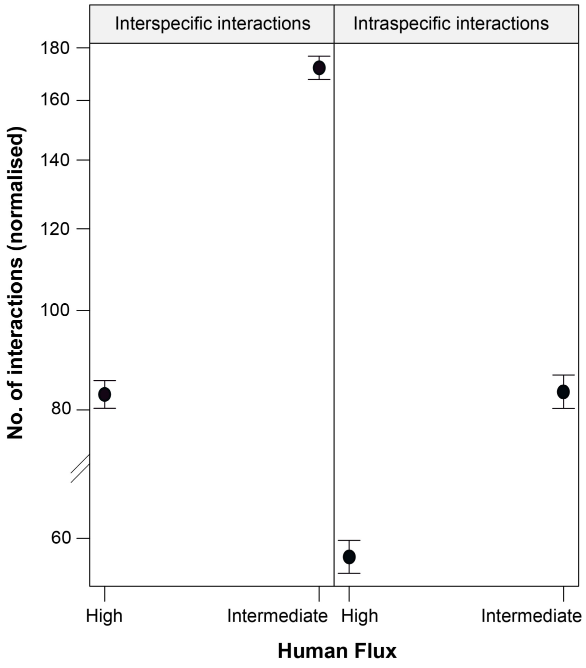

FIGURE 4 | An effect plot showing the interactive effect of human flux (high and intermediate) and type of interactions (intraspecific and interspecific), predicting the number of instances of such interactions. Solid circles and whiskers indicate the mean values and standard errors, respectively.

TABLE 5 | Generalized linear model showing the interactive effects of human flux zones and types of NCI^D on the values of NCI^D.

Fixed effects	Estimate	Std. error	*z*-value	Pr(>| *z*|)
Intercept	4.057565	0.053683	75.584	<2e-16***
NCI^D type "NCI^D_{Out}"	0.301278	0.070810	4.255	2.09e-05***
Human flux "intermediate"	0.008608	0.07575	0.114	0.90953
NCI^D_{Out} * intermediate	−0.29558	0.103499	−2.856	0.00429**

***p = 0.001, ***p = 0.*

Previous studies investigating dog–human interactions have suggested pet dogs' inclination toward preferring a human partner over conspecifics (Kaminski and Marshall-Pescini, 2014; Bräuer, 2015; Nagasawa et al., 2015). However, in free-ranging dogs, intraspecific interactions are necessary for maintaining group stability, defending territories, and other social behaviors, for example, parental care (Pal et al., 1998; Pal, 2003; Bonanni and Cafazzo, 2014; Paul et al., 2014a,b, 2015, 2017). Additionally, a substantial amount of negative human impact has also been suggested (Paul et al., 2016). Similar to other species living in urban habitats, a general aversion toward humans was thus expected (Raussi, 2003; Rodewald and Shustack, 2008; Carrete and Tella, 2011). Hence, it was surprising to observe higher interspecific than intraspecific interactions in these dogs. A recent study also concluded that domestication had shaped free-ranging dogs' behavior in terms of their tendencies to be in proximity to humans despite their limited socialization experience with humans than pets (Lazzaroni et al., 2020). We speculate that the interactions among conspecifics of a free-ranging dog group may be maintained using subtle behavioral cues. Thus, in a way, they might prefer being in the closeness of conspecifics without showing much direct behavioral interactions. Exploratory studies would be required to understand the presence of such subtle cues (if any) and the underlying dynamics better.

Dog–human relationships have been shown to vary within and across social contexts (Serpell, 2016). Though human flux could not predict the dog and human-initiated positive and

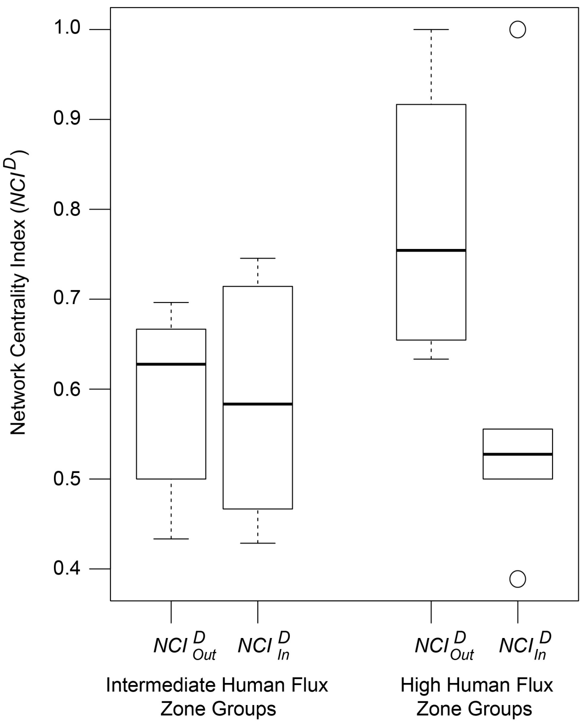

FIGURE 5 | A box and whisker plot showing the Network Centrality Index (NCI^D) values of the social networks. Boxes represent the interquartile range, horizontal bars within boxes indicate median values, and whiskers represent the upper range of the data.

TABLE 6 | Generalized linear model showing the interactive effects of initiator, and the type of behavior initiated, on the number of interactions.

Fixed effects	Estimate	Std. error	*z*-value	Pr(>|*z*|)
Intercept	−1.15787	0.39591	−2.925	0.00345**
Initiator "Human"	3.77767	0.38226	9.882	<2e-16***
Type of behavior "Positive"	2.04307	0.40172	5.086	3.66e-07***
Zone "Intermediate"	0.10053	0.08517	1.180	0.23785
"Human" * "Positive"	−2.13904	0.41017	−5.215	1.84e-07***

$^{**}p = 0.001$, $^{***}p = 0$.

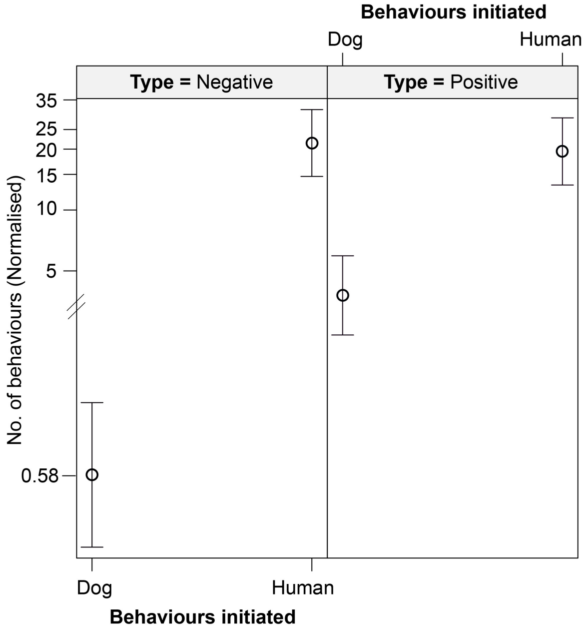

FIGURE 6 | An effect plot showing the interactive effect of type of behavior initiated (positive and negative) and initiator (dog and human), predicting the number of interspecific interactions. Solid circles and whiskers indicate the mean values and standard errors, respectively.

negative behaviors toward each other, humans were indeed found to be controlling the network dynamics in the high flux zones. Moreover, investigating the behavior of a species that interacts with humans could be useful to predict the perception or the influence of humans on that species. The differential results of the network properties in the two human flux zones, thus, may be attributed to varying anthropogenic impact on free-ranging dogs. For example, it is known that a personality trait like sociability (Sloan Wilson et al., 1994; Tuomainen and Candolin, 2011), is likely to be shaped by differential human actions through variable ontogenic experiences. As mentioned earlier, free-ranging dogs differ in their sociability behavior with regard to varying human flux (Bhattacharjee et al., 2020a); in crowded areas, dogs are typically exposed to a lot of unfamiliar humans which may eventually facilitate opportunistic begging, while also exposing the dogs to more frequent threats and aggression in other forms from humans. On the contrary, intermediate human flux zones represent areas where dogs encounter less number of unfamiliar humans. It is also important to note that the high human flux zones allow significantly higher access to potential food resources for these dogs than the intermediate ones (Bhattacharjee and Bhadra, under prep.). Unraveling the various factors concerning dog–human interactions will require future studies.

One potential shortcoming of the study was a restricted approach of analysis based on the "initiated" behaviors. We deliberately used the method to have initial baseline information on the dog and human-initiated behaviors toward each other. Further assessment of two-way interactions could be useful to complete the picture in future with more observational studies in specific directions. This is a first attempt to quantify direct interactions between dogs and humans on the Indian streets, providing significant inputs on the scantily explored topic of the free-ranging dog–human relationship. In India, dog–human conflict is a burgeoning issue (Kumar and Paliwal, 2015; Home et al., 2017) which attracts very harsh reactions, and immediate steps are required to curb this. While the law permits animal birth control as the solution to the growing dog population and the mitigation of conflict, this has not yet proven to be a feasible option in a country as large as India. Hence, efficient management of free-ranging dog populations requires a good understanding of their behavior, especially their interactions with humans. Findings from our study may be beneficial in terms of designing better management strategies and mitigation measures for such conflict.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by IISER Kolkata Animal Ethics Committee (approval no. 1385/ac/10/CPCSEA).

AUTHOR CONTRIBUTIONS

DB and AB designed and conceived the study. DB carried out the fieldwork and analyzed the data. DB wrote the first draft of the manuscript. AB edited the manuscript and supervised the entire work. Both authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.02153/full#supplementary-material

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Considering Family Dog Attachment Bonds: Do Dog-Parent Attachments Predict Dog-Child Attachment Outcomes in Animal-Assisted Interventions?

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Animal-Assisted Interventions (AAI) have become more prevalent in recent years, with dog-assisted interventions among the most popular. The literature suggests that a variety of dog-human interventions have the potential for beneficial outcomes for human participants and owners, however, critical gaps in knowledge still exist. Research addressing intervention outcomes for dogs, and the impact of AAI on the dog-human bond, has lagged behind. Even less is known about how dogs perceive child partners in AAI settings. The current study, which involved AAI for youth with developmental disabilities and their family dog, aimed to determine if the dog's style of attachment to a primary adult caretaker in the home was predictive of dog-child attachment style pre-and post-intervention. Using a Secure Base Test (SBT), the attachment style of the family dog toward an adult owner/parent was evaluated, and the attachment style of the dog toward the participating child was assessed before and after the dog-assisted interventions. The dog's attachment style to the child was then compared to the dog-parent attachment style. The findings show that all dogs with a secure attachment to the child at the initial assessment also had a secure attachment to the parent. It was also demonstrated that AAI has the potential to change the attachment style between a family dog and child to a more secure attachment, and that the dog-parent attachment style is a significant predictor of which dogs were able to develop a secure attachment to the child over the course of the AAI.

Keywords: human-animal interaction, animal-assisted intervention, Do As I Do, attachment, Secure Base Test, dog, family, children

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INTRODUCTION

Animal-Assisted Interventions (AAI) have increased in prevalence in recent years (Julius et al., 2013; O'Haire, 2017). Consequently, there has been increased research on the effectiveness and efficacy of different AAI approaches and predictors of outcomes across different populations (O'Haire, 2017; Hu et al., 2018; Jones et al., 2019; Chitic et al., 2020). Dog-assisted interventions are among the most common AAI, likely due to a number of factors including, but not limited to, a dog's accessibility, trainability, cost of care, and size (Linder et al., 2018). Critical gaps in knowledge about factors that may lead to successful AAIs still exist (O'Haire, 2017; Wanser and Udell, 2019; Wanser et al., 2019; Chitic et al., 2020). For example, little research has focused on the dog's perception of, or response to, the human participant or the intervention experience. This factor could play an important role in the efficacy of the dog's performance in the intervention and have implications for the wellbeing of both the dog and the human. How the dog perceives and responds to the human participant may be especially important for AAIs designed for children, including children with disabilities (Wanser et al., 2019). Animals, including dogs, have been known to respond in less predictable ways in the presence of these populations which can in some cases lead to increased risk (Overall and Love, 2001; Yin, 2011). Nevertheless, dogs are commonly used in therapeutic settings and interventions with both children and individuals with disabilities (Leonardi et al., 2017; Jones et al., 2019). Less is known about why some dog-child pairs clash (e.g., specific stimuli, strained interaction history, etc.) and others form successful relationships in home and/or intervention settings.

One factor that may be particularly relevant is attachment. Attachment can be defined as a bond that forms between two individuals, often a dependent individual (child or animal) and their caregiver, that promotes contact- and proximity-seeking, as well as stress reduction and facilitation of independent behavior in the case of secure attachments (Bowlby, 1958; Harlow, 1958). Research has demonstrated that dogs can form attachment bonds to their human caregivers (Topál et al., 1998; Palmer and Custance, 2008; Mariti et al., 2013) and humans can form attachment bonds to their dogs (Barker and Barker, 1988; Cohen, 2002; Kurdek, 2009). Once established, these bonds have the potential to benefit both the animal (Serpell and Barrett, 1995) and human with the strength and quality of attachment (e.g., attachment style) serving as predictive variables for health and welfare outcomes (Garrity et al., 1989; Rooney and Bradshaw, 2002; Bennett and Rohlf, 2007; Meyer and Forkman, 2014; Wanser et al., 2019). Furthermore, it is possible that the influence of AAI's conducted with a participant's own pet could be impacted by the nature and strength of the pre-established bond between the participant and animal (Wanser et al., 2019), or that participation in an AAI could alter the quality of the dyad's attachment bond, potentially in both the AAI and home settings.

When considering attachment quality, a range of different styles of attachment have been identified, which can broadly be divided into secure and insecure attachment styles. Individuals with secure attachment bonds can more effectively use their caretaker to reduce stress and display contact-exploration balance (Secure Base Effect) that allows them to explore and engage effectively in novel contexts and environments (Bowlby, 1958; Julius et al., 2013). Individuals with insecure attachments are still bonded to their caretaker, but this bond does not as readily facilitate stress reduction or a return to normal behavior in novel contexts (Bowlby, 1982; Ainsworth, 1989; Julius et al., 2013). There is currently some evidence that a dog's attachment style toward their caretaker may influence their performance in AAI contexts (Wanser and Udell, 2019; Wanser et al., 2019). For example, in one Animal-Assisted Activity (AAA) study, the attachment style between a trained therapy dog and their handler/caretaker was evaluated prior to a mock therapy session. Dogs behaved similarly toward their handlers and toward the mock therapy participants independent of attachment style with one exception: Dogs with an insecure attachment to their handler spent more time gazing back at that handler (and consequently less time gazing at the therapy participant) during the session compared to securely attached dogs. Such factors could influence therapeutic outcomes, and could also indicate that securely attached dogs may have lower stress levels during at least some forms of AAA sessions compared to those with insecure attachments (Wanser and Udell, 2019).

Oftentimes dogs who participate in AAI are handled by their owner and engage with unfamiliar AAI participants (as in the abovementioned study), but other times AAI can involve a human participant engaging with a familiar dog, especially in AAI targeted for children and their family pet dog (Tepfer et al., 2017). In such cases, understanding the possible connection between attachment quality and AAI participation could help predict the likelihood of achieving social support and other beneficial outcomes across settings. For example, it has been shown that a human participant's feelings of attachment toward a dog during AAI promotes participation in the intervention, including greater motivation to attend and greater pro-social engagement (Jones et al., 2019). Thus, one goal of dog-assisted interventions with children might be to establish or promote secure attachments between the dog and child engaged in AAI given the associated benefits reported in cases where stronger attachment relationships are perceived or exist. However, currently, little research exists on dog attachment bonds to children (Wanser et al., 2019). While it has been established that dogs can form attachment to one or more human caregivers (Topál et al., 1998; Gácsi et al., 2001; Parthasarathy and Crowell-Davis, 2006; Mariti et al., 2011, 2013), dogs do not form an attachment, much less a secure attachment, to every human they interact with (Thielke and Udell, 2020). While it is possible that a child in the same household may serve as an attachment figure for a family dog (Wanser et al., 2019), other (non-caregiver attachment) bond types may also be possible. For example, in humans, siblings that engage in caretaking behavior sometimes serve as attachment figures for younger children. However, siblings that do not engage in protective or caregiving behavior typically do not serve as primary attachment figures (Stewart, 1983). Nonetheless, siblings may share other forms of bond (Stewart, 1983). Therefore, it is possible that not all children will serve as a primary attachment figure for a dog in their household, even if they have developed some form of bond. In cases where a caregiver type bond is established between dog and child, the quality of attachment will likely vary between dyads (Wanser et al., 2019). Therefore, it is important to consider the style, or quality, of attachment relationship between dog and child, not just the presence or absence of a bond.

It is common for adults to be the primary caretakers of family dogs (Hall et al., 2016), which may be one reason the majority of work on dog-human attachment has focused on the relationship between dogs and their primary adult owner. However, evidence from the human literature suggests that the establishment of a secure attachment style to a primary caretaker can influence the strength and security of attachments formed with other individuals (Simpson, 1990; Maccoby, 1992; Smyke et al., 2010). Therefore, the attachment style of dog-adult owner pairs may also be a relevant consideration in AAI applications with child participants, as the quality of this primary attachment relationship could potentially predict (1) therapeutic or intervention performance directly (Wanser and Udell, 2019) and/or (2) the likelihood of secure attachment development between dog and child (Simpson, 1990; Maccoby, 1992; Smyke et al., 2010).

To our knowledge, no research to date has compared a dog's attachment bonds with both adult and child family members within a household. The influences of AAI participation on the dog's attachment behavior toward a child participant have also not been evaluated. Given that human-dog attachment has been shown to influence both human therapeutic outcomes and dog behavior in AAI settings, when considering AAI with children and family pet dogs, it may also be important to ask how pre-existing relationships between the dog and adult caretaker in the home could influence the dog-child bond and AAI motivation and performance, as well as how AAI influences the dog-human bond.

PILOT STUDY

The purpose of this initial study was to (1) evaluate attachment styles between dog-child dyads within an AAI setting across assessment time points to see to what extent secure attachments exist in this setting and (2) determine if a relationship existed between a dog's attachment style to an adult owner/parent in the household and to the child participant. We predicted that at least some dog-child dyads would display a secure attachment style. However, based on human attachment style research (Smyke et al., 2010), we predicted that dogs showing a secure attachment to an adult owner/parent would be more likely to show or develop a secure attachment to the child participant. As with other pro-social outcomes in prior AAA research (Tepfer et al., 2017), we predicted that the attachment style of dogs would either remain constant or become more secure over the course of AAI participation.

Methods

Participants

Seven youth with developmental disabilities and their parent were recruited to participate in this study with their family dog (see **Table 1**). Parents completed a demographic questionnaire to indicate their child's specific disability (no clinical assessments were conducted during the course of the AAI itself).

TABLE 1 | Participant demographic information for Pilot Study.

Child participants (*n* = 7)	
Age (years)	Range = 9–16; Mean = 12.7; SD = 2.9
Sex	Female = 5; Male = 2
Race	White = 6; Asian/Pacific Islander = 1
Primary Disability	Cerebral Palsy = 5; ADHD = 2
Parent participants (*n* = 7)	
Sex	Female = 7; Male = 0
Dog participants (*n* = 7)	
Age (years)	Range = 1–7; Mean = 3.4; SD = 2.5
Sex	Female = 5; Male = 2
Breed	Labrador Retriever = 2; Labrador Retriever mix = 1; Goldendoodle = 1; Golden Retriever = 1; Chihuahua = 1; Pomeranian = 1

Ethical Note

All children, parents, and dogs participated on a voluntary basis. Written informed consent was obtained from the parents/guardians of all participants, and assent was obtained from all of the children explicitly indicating their understanding and desire to participate in the research. The Institutional Review Board (IRB) and Institutional Animal Care and Use Committee (IACUC) of Oregon State University approved all methods and procedures for this study.

Intervention

Youth participants, identified as having a developmental disability, and their family dog were recruited from the northwestern region of the United States to participate in an animal-assisted intervention focused on joint physical activity. The AAI consisted of one session per week for 8 weeks, at a veterinary teaching hospital. Weekly AAI activities, led by a trained research assistant, consisted of joint physical activities for the child-dog dyad that were developmentally appropriate and tailored to the child's skills. For example, children might work on sit-to-stand skills and these were jointly completed by the child and their family dog for 10–15 repetitions. Other activities included jointly balancing on a wobble board, walking, playing catch together, and participating in cavalettis (i.e., small jumps). For homework the child participants were instructed to walk their dog for 30 min and practice the intervention exercises with the dog around the same time every day. This was intended to help establish a bond, create a habitual routine, and foster prompting behavior in the dog (e.g., attention-getting/walk-oriented behavior around the established time). A more detailed description of the intervention methodology, including intervention exercise descriptions has previously been published (please see Tepfer et al., 2017 for a review). Assessments were conducted with the participant-dog dyads before and after the 8-week intervention, as well as 6-months later.

Secure Base Test

The Secure Base Test (SBT) was used to evaluate the attachment behavior of the family dog toward both the child participant and adult owner/parent at the initial and follow-up assessments. This test was originally developed to assess the quality of attachment of non-humans to attachment figures (Harlow, 1958) and has been used to evaluate dog-human attachment style and security across multiple settings

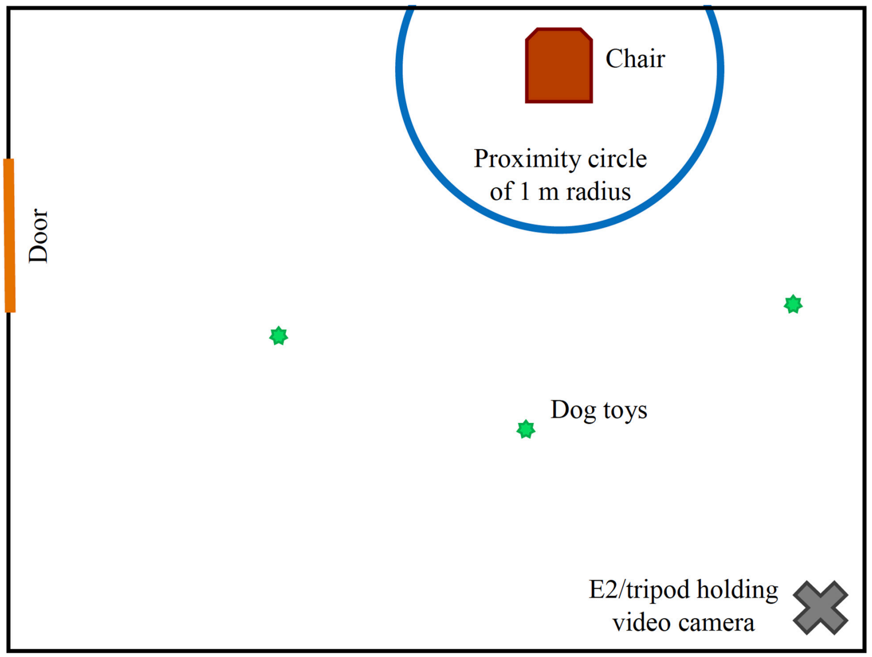

FIGURE 1 | Diagram of room set-up for Secure Base Test.

(Thielke et al., 2017; Thielke and Udell, 2019, 2020), including Animal Assisted Activities (Wanser and Udell, 2019) and was therefore especially well-suited to evaluate attachment style in the current study. Assessments were conducted in a room that was novel to the dog and human participants prior to testing. One chair was located inside a marked circle of 1-m radius on the floor, along a wall adjacent to the door (see **Figure 1**). Three toys – tennis ball, rope toy, and plush-squeak toy – were on the floor outside the circle. Two experimenters (E1 and E2) conducted the test. E1 provided instructions at the start of each phase to ensure consistent participant behavior (E1 remained outside of the room during all phases). E2 stood neutrally/inattentively in a corner of the room controlling the video camera (except during the alone phase when the camera was left on a tripod). The SBT was divided into three two-minute phases:

Baseline/habituation phase

The experimenter led the dog and the human participant (i.e., child or parent) into the room and indicated for them to remove the dog's leash and sit in the chair. The human participant was instructed that when the dog entered the circle surrounding their chair, they could interact with the dog (i.e., talking/petting/playing), but when the dog was outside the circle, they must remain silent, passive, and non-moving.

Alone phase

E1 opened the door to indicate to the human participant to exit the room. E2 left the camera on the tripod filming toward the door and also exited, leaving the dog alone. The alone phase serves as a mild stressor, allowing for assessment of the Secure Base Effect during the return phase.

Return/experimental phase

E1 directed the human participant to enter the room and follow the same instructions as the baseline phase. E2 followed closely behind the participant in entering the room and returned to the corner to control the camera, without any interaction with the dog.

Behavior Coding

All assessments were video recorded. The return phase was viewed by two coders, with prior training in evaluating canine attachment styles. These two coders independently categorized the dogs' behavior using an ethogram for canine attachment style categories and definitions previously established in the literature (Schöberl et al., 2016; Thielke et al., 2017; Thielke and Udell, 2019, 2020; Vitale et al., 2019; Wanser and Udell, 2019): secure, insecure ambivalent, insecure avoidant, and insecure disorganized (see **Table 2**). Inter-rater reliability was then assessed for the full data set (75.7% IRR for attachment style categorization, binomial probability test, $p < 0.001$). After independent IRR analysis, categorization disagreements were then jointly reviewed to come to consensus for the final attachment style designation using the standard procedure for holistic canine attachment style categorization (Thielke et al., 2017; Thielke and Udell, 2019, 2020; Wanser and Udell, 2019). The broader categorization of secure or insecure attachment, indicating the presence or absence of the Secure Base Effect, was the primary focus in this study.

Results and Discussion

The dog-child attachment style changed from an insecure style pre-intervention to a secure style post-intervention in

TABLE 2 | Canine attachment style definitions (adapted from Schöberl et al., 2016 and Thielke et al., 2017).

Attachment Style	Definition
Secure	Dog's greeting behavior is active, open, and positive. Little or no resistance to contact or interaction with the human participant. Seeks proximity and is comforted upon reunion, returning to exploration or play.
Insecure Ambivalent	Dog shows exaggerated proximity-seeking and clinging behavior (but may struggle if held by human participant). Exhibits a mix of persistent distress with efforts to maintain physical contact with the human participant and/or physically intrusive behavior toward the human participant (Dogs who the judges agreed seemed essentially secure but with ambivalent tendencies were categorized as secure).
Insecure Avoidant	Dog shows little or no visible response to the human participant's return. Ignores or turns away from human participant but may not resist interaction altogether (e.g., laying, sitting, or standing without physical contact with, out of reach of, or at a distance from human participant).
Insecure Disorganized	Dog exhibits evidence of a strong approach-avoidance conflict or fear upon reunion (e.g., circling human participant, hiding from sight, rapidly dashing away upon reunion, or "aimless" wandering around the room). A lack of coherent strategy is shown by contradictory behavior. Dog may show stereotypies upon reunion (e.g., freezing or compulsive grooming). "Dissociation" may be observed, that is, still or frozen posture, staring into space without apparent cause, for at least 20 s (in a non-resting, non-sleeping dog).
Unclassifiable*	Judges were unable to reach consensus on the attachment style categorization of the dog. Unclassifiable dogs were excluded from further analysis on dog attachment.

**No dogs in the current study were unclassifiable.*

two instances. Two dogs displayed a secure attachment to their child pre- and post-intervention, and the remaining three dogs displayed insecure attachments to the child both pre- and post-intervention. The dog-parent attachment style was a strong predictor of whether a secure attachment style was present or would develop between the dog and child during the intervention (Fisher's Exact Test, $p = 0.03$). Four dogs were categorized as having a secure attachment to the adult owner/parent, and also had or developed a secure attachment toward the child by the last assessment. The remaining three dogs displayed an insecure attachment to the adult owner/parent and remained insecurely attached to the child throughout the study.

While the population under test in this initial pilot study was small, it still identified statistically significant differences that would suggests that AAI participation has the potential to improve human-animal interactions and, critically, the dog-parent attachment style was a significant predictor of which dogs were able to develop a secure attachment to their child partner during AAI. This is consistent with attachment research in human infants, where individuals with secure attachments to primary caregivers or foster parents facilitated secure attachment development to future attachment figures or adoptive parents (Smyke et al., 2010).

AAI EXPERIMENT

In this AAI Experiment, we sought to explore whether the findings of our pilot study would be generalized in the context of a novel AAI setting with a larger sample size.

Methods

Participants

Twenty-four youth with developmental disabilities and their parent were recruited to participate in this study with their family dog (see **Table 3**). Parents completed a demographic questionnaire to indicate their child's specific disability (no clinical assessments were conducted during the course of the AAI itself). Two pairs of siblings participated and shared the same dog and parent between them. Thus, twenty-two pet dogs and twenty-two parents participated in this study.

Ethical Note

All children, parents, and dogs participated on a voluntary basis. Written informed consent was obtained from the parents/guardians of all participants, and assent was obtained from all of the children explicitly indicating their understanding and desire to participate in the research. The Institutional Review Board (IRB) and Institutional Animal Care and Use Committee (IACUC) of Oregon State University approved all methods and procedures for this study.

Intervention

Families were recruited from the northwestern region of the United States to participate in a randomized control study involving synchronous activity-based AAI for youth with developmental disabilities. For the current study we focused on 24 child-dog dyads randomly assigned to one of two AAI groups [12 participated in a "Do As I Do" dog training intervention

TABLE 3 | Participant demographic information for AAI Experiment.

Child participants (n = 24)	
Age (years)	Range = 8–17; Mean = 11.3; SD = 2.5
Sex	Female = 10; Male = 14
Race	White = 19; Latino/Hispanic = 2; Alaskan Native = 2; unknown = 1
Primary Disability	Autism Spectrum Disorder = 7; ADHD = 5; Intellectual Disability = 4; Down Syndrome = 2; Fetal Alcohol Spectrum Disorders = 2; Anxiety Disorder = 2; Specific Learning Disability = 1; Physical Disability = 1
Parent participants (n = 22)	
Sex	Female = 17; Male = 5
Dog participants (n = 22)	
Age (years)	Range = 0.4–10; Mean = 3.0; SD = 3.0
Sex	Female = 14; Male = 8
Breed	Goldendoodle = 3; Golden Retriever = 2; Poodle mix = 2; Labrador Retriever mix = 2; Labrador Retriever = 1; Standard Poodle = 1; Miniature Poodle = 1; Toy Poodle = 1; Alaskan Husky = 1; Australian Shepherd = 1; Australian Shepherd mix = 1; Beagle = 1; Brittany Spaniel = 1; Chihuahua = 1; Great Dane = 1; Rough Collie = 1; Whippet mix = 1

(Fugazza, 2014) and 12 in a dog walking intervention]. Both the dog training and dog walking interventions were conducted in ten 1-h sessions on a university campus. During the summer the interventions were offered 5 days per week for 2 weeks and during the school year the interventions were offered 2 days per week for 5 weeks. A pair of trained research assistants worked with each participant-dog dyad for all ten sessions, coaching the child on how to train their dog on the objectives of the study group to which they were assigned (i.e., "Do As I Do" training or leash walking). At home participants were instructed to walk their dog for 30 min and work on the intervention training skills with their dog for 5 min every day as homework throughout the course of the intervention. Assessments were conducted with all participant-dog dyads during the week prior to the start of the intervention and the week after the end of the intervention.

Secure Base Test

As in the pilot study, the SBT was used to evaluate the attachment behavior of the family dog toward the child participant at the initial and follow-up assessments. The SBT was also used to evaluate the attachment behavior exhibited by the dog toward an adult owner/parent for comparison to the dog's behavior toward the child. The same methodology was used across both studies.

Behavior Coding

As in the pilot study, all assessments were video recorded and the return phase was viewed by two coders who independently categorized the dog's behavior using an established ethogram for canine attachment style categories (**Table 2**). There was 68.6% independent inter-rater agreement for attachment style categorization (binomial probability, $p < 0.001$). Categorization disagreements were then jointly reviewed to come to consensus for the final attachment style designation. The broader categorization of secure or insecure attachment, indicating the presence or absence of the Secure Base Effect, was the primary focus in this study.

Results and Discussion

Similar to what was observed in the pilot study, nine dogs exhibited a secure attachment to the child and 18 dogs exhibited a secure attachment to the parent. All nine dogs with a secure attachment to the child also had a secure attachment to the parent (Binomial Test, $p = 0.004$). No dogs with an insecure attachment to the parent ($n = 6$) had a secure attachment to the child (Binomial Test, $p = 0.03$).

At the follow-up assessment, 18 dogs had a secure attachment to the child. This was a statistically significant increase in the number of secure attachment bonds between dog and child participants when comparing pre- and post-intervention attachment styles (Fisher's Exact Test, $p = 0.02$). In addition, 15 of those 18 dogs also had a secure attachment to the parent (Binomial Test, $p = 0.008$), suggesting that while some dogs can form a secure attachment to the child partner post-intervention without having a secure attachment to the primary caregiver (in this case 3 dogs), a secure attachment to the parent still appeared to be a significant predictive variable. No dogs shifted from a secure attachment style toward the child pre-intervention to an insecure attachment style post-intervention, again supporting prior findings that participation in this kind of AAI typically has a neutral to beneficial impact on the dog-human bond (Tepfer et al., 2017).

GENERAL DISCUSSION

Research indicates that the bonds between dogs and adult owners can fulfill the criteria of an attachment bond (Topál et al., 1998; Palmer and Custance, 2008; Mariti et al., 2013), and some studies have gone on to categorize dogs into formal attachment styles (Schöberl et al., 2016; Thielke et al., 2017). The current findings demonstrate that, in at least some cases, dogs can also form a secure attachment bond to a child in the household. Furthermore, in these two studies, the attachment quality between dog and child was predicted by the attachment style of the dog toward a primary adult caregiver. Participation in a joint activity-based AAI also helped improve the attachment security of the dog-child bond in some cases. These findings shed light on how dogs may perceive children in their environment, in what ways relationships with other bonded humans influences this perception and how participation in joint interventions with a child partner can impact the dog-child bond.

In many households the primary caregiver and attachment figure of the family dog is an adult owner (Hall et al., 2016). Therefore, it is not surprising that more secure attachments were observed between the dogs and adult owners than between dogs and children during initial assessments. However, it is common for both humans and dogs to have multiple attachment figures (Topál et al., 1998; Howes and Spieker, 2008; Kurdek, 2009; Mariti et al., 2011), and the current findings demonstrate that secure attachments between a dog and a child in the same household may exist prior to, or develop during, a child-focused AAI. Moreover, the present results support prior evidence from the human literature that the establishment of a secure attachment style to primary caregivers can influence the strength and security of attachments formed with other individuals (Simpson, 1990; Maccoby, 1992; Smyke et al., 2010), in this case children in the same household. While more research is needed to determine the full range of variables that may contribute to secure attachment development between dogs and children in the household, it seems promising that AAIs developed with joint participation and mutual well-being in mind have the potential to improve attachment bonds between human and animal participants.

Evidence of secure attachment development between dog-child AAI partners has a number of important applied implications. For example, secure attachments have been shown to have a wide range of benefits including stress reduction, increased exploration and persistence, improved executive function, and a reduction of behavior problems in dogs and humans (Bowlby, 1982; de Ruiter and van IJzendoorn, 1993; Cooper et al., 1998; Horn et al., 2013; Bernier et al., 2015). When the child becomes a secure base for a dog AAI partner, this could also enhance the dog's sense of security to engage in the environment alongside the child (Julius et al., 2013), possibly improving the animal's welfare, focus, or performance in the AAI (Wanser and Udell, 2019). Changes in the dog's behavior may increase a child's perceptions of their own attachment toward their dog, which can also have a positive effect on wellbeing and AAI outcomes (Hall et al., 2016; Wanser et al., 2019). For example, the dog may seek out the child more for interaction at home when the parent is absent/unavailable, fostering increased interactions and greater feelings of responsibility and companionship for the child. Additional research is needed to evaluate these possibilities, and to expand on the current findings. Future research should also evaluate additional behavioral differences in securely attached dogs toward AAI partners who double as caretakers, as benefits may extend beyond those already identified in therapeutic settings with visiting therapy dogs (Wanser and Udell, 2019). However, the knowledge that at least some AAIs can have a beneficial impact on the dog-human relationship – and more specifically the dog-child relationship (with no evidence of a negative impact identified in the current study) – is a promising finding that supports the One-Health mission of many AAI efforts. More research will help improve our understanding of how the dog-human bond may influence AAI outcomes, to identify ways to maximize the health and wellbeing of animal and human participants, as well as to improve human-animal interactions in AAI settings. Furthermore, research focused on the child-dog bond may provide important insights into similarities and differences in the ways dogs and children perceive one another (compared with dog-adult human relationships), interact together, and in some cases, serve as support to one another within the home and in AAI settings.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Institutional Review Board (IRB) of Oregon State University. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. The animal study was reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) of Oregon State University. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

MU and MM conceived and planned both studies. SW, MU, and MM carried out the pilot study. SW, AS, MU, and MM carried out the AAI Experiment. SW and MU analyzed the data and wrote the manuscript with contributions from AS and MM. All authors contributed to the article and approved the submitted version.

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The reviewer AB declared a past co-authorship with one of the authors MU to the handling editor.

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Visual Attention Patterns Differ in Dog vs. Cat Interactions With Children With Typical Development or Autism Spectrum Disorders

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Visual social attention is an important part of the social life of many species, including humans, but its patterning may vary between species. Studies on human–pet relationships have revealed that visual attention is also part of such interspecific interactions and that pets are sensitive to the human visual attentional state. It has been argued that domestication and/or repeated experiences with humans have shaped and refined these decoding abilities. Little is known on how the species' evolutionary history may play a role in determining visual attention patterns during interactions, nor how the human's own social skills may influence the animal's attention patterns in human–animal interactions. In the present study, we investigated the visual attention patterns directed to the partner in dog–child and cat–child interactions in their home environment. We also compared these patterns between a group of children with autism spectrum disorders (ASD) and children with typical development. We found that the attention patterns differed according to species, with dogs displaying more gazes and cats more glances toward their human interlocutor, while children showed gazes toward both species. Only slight differences were observed according to the developmental status of children: ASD children displayed much more visual attention with their pet cat than with their pet dog and the same amount of visual attention toward their pet, whatever the species, as typically developing (TD) children. Because humans rely a lot upon visual communication in their own social encounters, where direct gazes play a major role from early on, they may be especially sensitive to the gazing behavior of their dogs. People with ASD, with a less typical pattern of interaction, may be more comfortable with the less "invasive" short glances of cats. These results suggest not only that interspecific communication has to be associated with processing and storing the other species' ways of communicating in order to be successful but also that visual attention patterns during interactions, even when interspecific, are, for a large part, the result of the species' own evolutionary history.

Keywords: human–pet interactions, social visual attention, autism, dogs, cats

INTRODUCTION

Social attention is one of the most important aspects of social life (Scheid et al., 2007), and according to Goffman (1961), attention is what makes the difference between a proper social interaction and a mere co-presence. Visual attention is in this regard an important component of social interaction in a variety of species (Snowdon and Hausberger, 1997; Lemasson and Hausberger, 2004). The pattern of visual attention may vary according to the species' social characteristics, from a "dominant-centered" visual focus to a "monitor-adjust" system of divided attention toward all group members in tolerant species (e.g., York and Rowell, 1988; Blois-Heulin and Girona, 1999; Lemasson et al., 2006). In corvids, jackdaws show more attention toward non-affiliates, whereas ravens spend more time gazing at friends (Scheid et al., 2007). There has been growing evidence that, in many species, far from being a mere threat signal as long thought, social gazing, and gaze following may reflect friendship (Hattori et al., 2007; Micheletta and Waller, 2012). In primates, affiliative and status relationships do affect how much individuals attend visually to others (Chance and Joly, 1970). Attention patterns also vary between species and according to context, favoring either short glances or durable gazes toward group members (Day et al., 2003). In humans, longer gazes (more than 1 s) correspond to the shift from a common focus on a topic of interest to a focused attention to the interlocutor, especially in the case of affiliative attraction (Kendon, 1967).

Visual attention is also an important part of interspecific communication, as observed in human–animal interactions. Domestic, but also captive wild animals, have been shown to present a sensitivity to human attentional states, especially through gaze direction (e.g., dogs: Call et al., 2003; Schwab and Huber, 2006; horses: Sankey et al., 2011; capuchin monkeys: Hattori et al., 2007; red-capped mangabeys: Maille et al., 2012). These abilities may reflect, in the first case, effects of domestication, i.e., selection of animals more skilled in decoding human cues, but also, in both domestic and wild captive animals, shared experiences during repeated interactions (e.g., Leroux et al., 2018). Humans also are very sensitive to their pet's visual attention, as shown recently: dog owners exhibit an increase of oxytocin as a result of their dogs showing long gazes toward them (Nagasawa et al., 2015). Although the sensitivity to human attentional state is widespread among domestic animals, the extent of this ability is different according to species and may well depend upon the evolutionary processes underlying the species' own social dispositions (Chance and Joly, 1970; Mason, 1978). Dogs and cats, for example, although both companion animals, differ in their level of distractibility, which could be explained by a better inhibitory control of cats which have a "sit and wait" predatory strategy (Kraus et al., 2014). Social canids may, on the other hand, rely upon visual contact between group members for hunting (e.g., Bekoff et al., 1984). In dogs, sustained gazes may reflect attempts of dominance ("staring"), but also affiliative behaviors (e.g., Bradshaw and Nott, 1995).

To our knowledge, there is no scientific information about how these two companion species differ in terms of visual attention in spontaneous interactions with humans. On the other hand, the human responses themselves may both depend upon the pet's behavior and their own human's attentional skills. Human infants, from the first days of life, follow other people's gaze and seek eye contact and mutual gazing, which are crucial for their development and long-term parent–child bonding (Scaife and Bruner, 1975; Farroni et al., 2002; Guellai et al., 2014).

However, social visual attention is impaired in some types of atypical development, e.g., autism spectrum disorders (ASD) (Goldstein et al., 2001; APA, 2013). People with ASD have difficulties in the perception of direct and indirect human gazes (Forgeot d'Arc et al., 2017) and a limited use of mutual gaze or joint attention during interactions with peers (Emery, 2000). They also display an atypical visual exploration of human face pictures, focusing mainly on the mouth part (Guillon et al., 2014). They show an increased arousal when submitted to a human direct gaze (O'Haire et al., 2015). Interestingly, a recent eye tracking study shows that ASD children look at eyes when animal faces are presented (Grandgeorge et al., 2016), as also suggested by numerous testimonies (Grandin and Johnson, 2005).

In the present study, we hypothesized that the visual attention patterns would differ during dog–child and cat–child interactions due to species differences in attentional and bonding characteristics. Dogs, as a social cooperative canid, are expected to exhibit more durable gazes and cats, as a solitary opportunistic gregarious species, more short glances. Moreover, we also investigated the impact of the human interlocutor *per se* on the dyad's pattern of visual attention by comparing a group involving children with typical development to another group involving ASD children, i.e., with altered visual social skills. Observations were performed in the home environment so as to have "ecological" data from already bonded interspecific partners. Questionnaires allowed us to additionally have the parents' perception of the quality of their child's interactions and bonding with their pet animal.

MATERIALS AND METHODS

Ethical Concern

Data were collected between 2009 and 2012, in accordance with the (at that time) current French legislation. As this research was observational, it required no ethics committee at this time. All the dogs and cats involved in the study were family pets, hence under their owners' responsibility for care and use. The researchers had no involvement in any decision in this regard, and the study was conducted in accordance with the French regulations governing the use of animals for research. Regarding humans, all parents provided free, informed, and written consent for the participation of their child in the study, all in accordance with the Declaration of Helsinki (6th revision), and French regulations at that time. The parents gave their written consent to allow us to film their child.

Participants

General Information

Forty-two children were recruited: they were all aged 6–12 years, had no prior parent-reported history of animal abuse, and had no physical disability that could limit their interactions with their dog or cat. Nineteen children with typical development were included after recruiting by adverts. Twenty-three children with ASD came from the "Centre de Ressources sur l'Autisme de Bretagne," CHRU Brest, Bohars, France. Behavioral assessments were performed using the Autism Diagnostic Interview – Revised (ADI-R) (Lord et al., 1994). The ADI-R, an extensive, semi-structured parental interview, was conducted by independent psychiatrists. The ADI-R scale assessed the three major domains of autistic impairments: reciprocal social interactions, verbal and non-verbal communication, and stereotypic behaviors and restricted interests. Based on direct clinical observations of each child by independent child psychiatrists, a diagnosis of ASD was made according to the DSM-IV (APA, 2000) and ICD-10 (World Health Organization, 1994) criteria and was confirmed by the ADI-R ratings. **Table 1** presents the sample populations.

Because the quality of the relationship may influence the pattern of visual attention, we used a parent-based short questionnaire to have an evaluation of it (see also Grandgeorge et al., 2012). This was represented by two items: information about the frequency of visual interaction between their child and their pet (according to a three-point Likert-scale: never, rarely, and often) and whether they considered the child–pet relationship as a "privileged" relationship, such as "favorite pet of the child, spending time and playing together and reciprocal behaviors") (defined by Grandgeorge et al., 2014).

Population 1: Pet Dogs and Associated Children

The population of pet dogs included 16 males (eight with children with ASD and eight with children with typical development) and 10 females (six with children with ASD and four with children with typical development), four mongrels and 22 purebreds, all adults (more than 18 months old) (**Table 1**).

The 26 children involved (**Table 2**) consisted of 14 children with ASD, all males (mean age = 10.1 ± 2.1 months), matched on chronological age with 12 children with typical development (eight boys and four girls, mean age = 9.4 ± 2.4 years) [Mann–Whitney test: $U_{(14,\ 12)} = 75.5$, $p = 0.680$].

Population 2: Pet Cats and the Associated Children

Sixteen pet cats were involved, corresponding to nine males (three with children with ASD and six with children with typical development) and seven females (five with children with ASD and two with children with typical development). Thirteen were mongrels and three others were purebred. Three were less than 1 year old (i.e., young, all with children with ASD) and 13 were adults (**Table 1**).

The 16 children (**Table 2**) corresponded to eight children with ASD, all males (mean age = 7.5 ± 2.2 years), matched on age with eight children with typical development (three boys and five girls, mean age = 9.0 ± 1.9 years) [Mann–Whitney test: $U_{(8,\ 8)} = 13$, $p = 0.160$].

Experimental Design

One-hour observation sessions were performed at the child's home. They were performed at fixed times (4–6 p.m.), when the children were back from school or institution. Before starting, the observer (MG) asked the child and the other people present (e.g., father, mother, and siblings) to behave as usual and made clear that no behavior was considered either good or bad. She carried a camera and filmed the child's behavior continuously (including interactions with the pet or with family members). She remained silent and did not take part in the interactions (MacGrew, 1972; Millot et al., 1988).

TABLE 1 | Characteristics of the pet population (young = under 1 year of age).

	Pet dog	Pet cat
N	26	16
Gender (M/F)	16/10	9/7
Age (young/adult)	0/26	3/13
Purebred/mixed breed/mongrels	22/0/4	3/0/13
Details about breeds	Large-sized mongrels, *n* = 1	Chartreux, *n* = 1
	Middle-sized mongrels, *n* = 3	Siamese, *n* = 2
	Border Collie, *n* = 1	Mongrels, *n* = 13
	Bernese mountain dog, *n* = 1	
	Boxer, *n* = 2	
	Cavalier King Charles spaniel, *n* = 3	
	Cocker spaniel, *n* = 1	
	Golden retriever, *n* = 3	
	Groenendael, *n* = 2	
	Jack Russel Terrier, *n* = 2	
	Labrador retriever, *n* = 4	
	Lhasa Apso, *n* = 1	
	Newfoundland dog, *n* = 1	
	Yorkshire terrier, *n* = 1	

TABLE 2 | Characteristics of the sample population of children.

	Living with pet dogs	Living with pet cats
Characteristics of the ASD children		
N	14	8
Mean age ± SD (in years)	10.1 ± 2.1	7.5 ± 2.2
Gender (M/F)	14/0	8/0
Privileged relationships (yes/no)	8/6	8/0
Frequency of visual interaction (according to parents)	7 often 5 rarely 2 "don't know"	4 often 3 rarely 1 "don't know"
Characteristics of the children with typical development		
N	12	8
Mean age ± SD (in years)	9.4 ± 2.4	9.0 ± 1.9
Gender (M/F)	8/4	3/5
Privileged relationships (yes/no)	9/3	6/2
Frequency of visual interaction (according to parents)	9 often 2 rarely 1 never	5 often 2 rarely 1 "don't know"

Data Collection

Behavioral data were sampled from the video recordings using continuous focal sampling. Behavioral data were only analyzed when both child and pet were visible on the video recording (Altmann, 1974). Different parameters of pet and child visual attention were measured and the initiator of the visual interaction was identified. Thus, occurrences and, when appropriate, durations (in seconds) were calculated for the following behavioral items:

- Glances: focusing eyes on the other partner at ± 5° for less than 1 s (Blois-Heulin and Girona, 1999).
- Gazes: focusing eyes on the other partner at ± 5° for at least 1 s.
- Mutual gazes: child's and pet's attention was directed to one another (Emery, 2000).

According to Emery (2000), several cues could be used to determine the direction of visual attention: when the eyes were little or not visible, the orientation of the head and/or body was used. If the eye direction was not clearly identified, it was recorded as non-visible.

All data analyses were performed by three observers (YG, YB, and HM), blind to the child diagnosis. Inter-observer reliability was ensured by training with one senior author (MG) until full agreement was reached.

Statistical Analyses

As data were not normally distributed, we used non-parametric statistical tests (Siegel and Castellan, 1988). As the duration of the children–pet visibility varied between video recordings, we homogenized all data by calculating the number of occurrences and the durations per minute. Mann–Whitney *U* tests were used to compare two independent samples (e.g., gaze duration toward the pet between the two groups of children). Wilcoxon signed-rank tests were used to compare dependent samples (e.g., children's gaze duration toward the pets compared to pet's gaze duration toward the same children). Spearman's tests were used to evaluate the correlations (e.g., between children's gaze occurrences and dog's gaze occurrences). These analyses were run with Statistica software and R software with an accepted *p* level at 0.05.

RESULTS

Visual Attention Between Dogs and Children

Pet Dogs

During the observation sessions, the child–dog dyads were visible around 50% of the video recording, whatever the child's status (ASD: 1,562.46 ± 937.23 s, TD: 2,084.67 ± 821.98 s, respectively, $U = 58$, $p = 0.189$).

Overall, there was no difference in the structure of visual attention between the TD and ASD groups for both children and pets (all Mann–Whitney tests: $p > 0.05$; **Figure 1A**): all dogs and children performed more gazes (mean occurrence: dogs, 2.48 ± 2.47 per minute; children, 2.38 ± 2.14 per minute) than glances (mean occurrence: dogs, 0.80 ± 1.18 per minute; children, 0.24 ± 0.19 per minute; $Z = 4.371$ and 4.284, respectively, $p < 0.001$).

In both groups, pet dogs more frequently initiated glances (but not gazes) toward the children than did the children toward the dogs (ASD group: 0.96 ± 1.55 vs. 0.2 ± 0.19 per minute, $W = 2.417$, $p = 0.016$; TD group: 0.61 ± 0.51 vs. 0.29 ± 0.19 per minute, $W = 2.045$, $p = 0.041$) (**Figure 1A**). Moreover, the visual attention displayed by the dogs and children were not correlated (whatever the children group, visual attention type, and measures; all Spearman's correlation, $p > 0.05$). Neither the frequency nor the duration of dog–child mutual gazes differed between groups (occurrence: ASD, 2.28 ± 3.18 s; TD, 2.34 ± 2.7 s, $U = 66$, $p = 0.374$; duration: ASD, 4.77 ± 3.44 s; TD, 5.55 ± 3.46 s, $U = 71$, $p = 0.520$, respectively).

Pet Cats

The cat–child dyads were visible only around 10% of the video recording for both the ASD and TD children groups (646.51 ± 335.90 and 605.53 ± 424.63 s, respectively, $U = 25$, $p = 0.495$).

Overall, the two groups did not differ in the structure of their visual attention: cats showed an equal proportion of glances and gazes in both cases (2.3 ± 1.6 and 2.1 ± 0.8 per minute, $Z = 0.451$, $p = 0.649$, respectively), whereas children – whatever their diagnostic group – displayed more gazes (mean occurrence: all children, 3.9 ± 1.3; ASD children, 3.5 ± 1.2; TD children, 4.3 ± 1.3 per minute) than glances (mean occurrence: all children, 1.8 ± 1.5; ASD children, 1.6 ± 1.1; TD children, 1.9 ± 1.8 per minute; $Z = 3.244$, $p = 0.001$) toward their pet. Mutual gazes were rare (mean occurrence, 0.7 ± 0.7 per minute; ASD children, 0.6 ± 0.6 per minute; TD children, 0.7 ± 0.8 per minute) and less frequent than unilateral gazes and glances both in children and pet cats (all Wilcoxon tests: $p < 0.001$).

Overall, there was no significant difference according to the child group, whether in children's or pets' attentional characteristics (glances, gazes, and mutual gazes; all tests: $p > 0.05$) (**Figure 1B**).

In both groups, the cats and children initiated glances (respectively, glances toward cats: for all children, 1.7 ± 1.5; for ASD children, 1.6 ± 1.1; for TD children, 1.9 ± 1.8 per minute; glances emitted by cats toward all children, 2.1 ± 1.6; toward ASD children, 1.8 ± 1.6; toward TD children, 2.3 ± 1.8 per minute) (**Figure 1B**) and mutual gazes (respectively, mutual gazes initiated by all children, 0.2 ± 0.3; by ASD children, 0.2 ± 0.3; by TD children, 0.2 ± 0.3; mutual gazes initiated by cats toward all children, 0.5 ± 0.5; toward ASD children, 0.4 ± 0.4; toward TD children, 0.5 ± 0.7 per minute (**Figure 1B**) equally often.

Finally, TD children initiated more frequent and longer gazes toward their pet cats than did their pet cats (4.3 ± 0.7 vs. 1.8 ± 0.7 per minute, $W = 34$, $p = 0.023$; 0.8 ± 0.5 vs. 0.3 ± 0.2 per minute, $W = 35$, $p = 0.016$) (**Figure 1B**), whereas no such difference was found in the ASD group (occurrence and duration: all Wilcoxon tests, $p > 0.05$). However, the visual attention displayed by the cats and children were not correlated (whatever

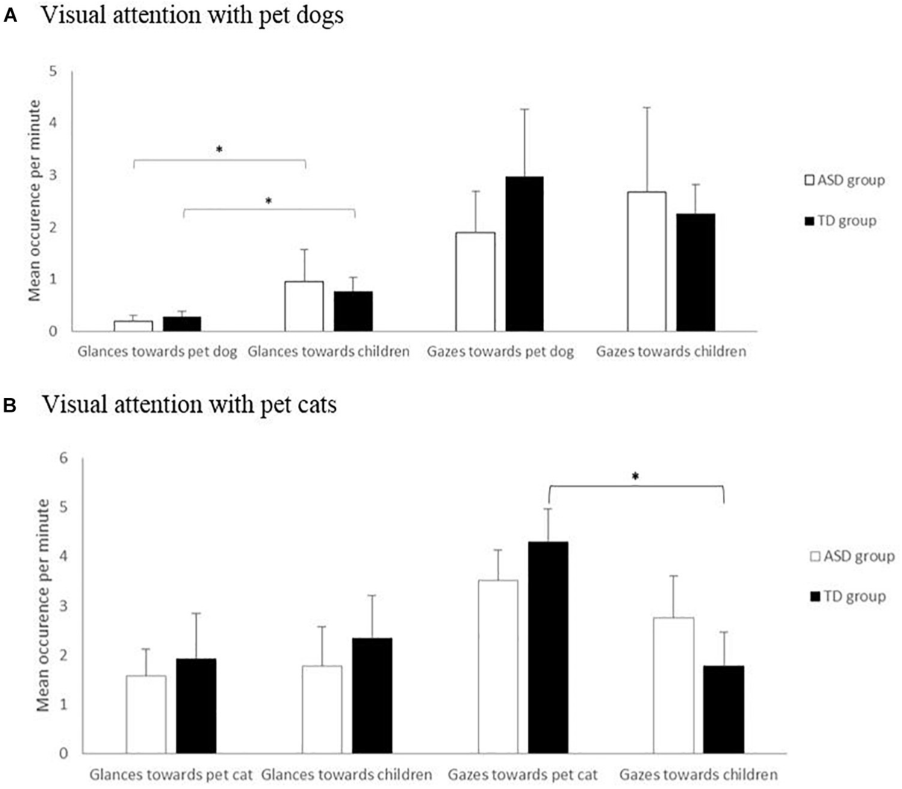

FIGURE 1 | Visual attention in the autism spectrum disorders (ASD) and typically developing (TD) groups in occurrence per minute (glances and gazes) in pet dog–child **(A)** and pet cat–child **(B)** dyads. Mann–Whitney and Wilcoxon tests. $^*p < 0.05$.

the children group, visual attention type, and measures: all Spearman's correlation, $p > 0.05$).

Differences of Visual Attention Patterns Between Pet Dog–Child Dyads vs. Pet Cat–Child Dyads

The structure of attention clearly differed according to the species in the TD group, with more glances from cats and more gazes from dogs ($U = 17$, $p = 0.019$ and $U = 11$, $p = 0.007$, respectively). On the contrary, no such difference in visual attention according to species could be evidenced in the ASD group ($U = 29$, $p = 0.103$; **Figure 2A**).

These findings were reflected in the children's patterns of attention as the TD children also glanced more at cats and gazed more at dogs ($U = 9$, $p = 0.030$ and $U = 20$, $p = 0.052$, respectively) (**Figure 2B**), whereas ASD children performed more visual attention overall, i.e., more gazes ($U = 26$, $p = 0.040$) and glances ($U = 4$, $p = 0.0006$) toward their cats than their dogs. Interestingly, these observational patterns were not reflected by parents' reports, which indicated that seven (out of 14, i.e., 50%) children with ASD and nine (out of 12, i.e., 75%) with TD had frequent visual interactions with their pet dogs and that four (30%) children with ASD and five (40%) with TD were considered as often having visual interaction with their pet cats. Thus, both children's groups were reported as having less visual interactions with cats than with dogs (gazes: $U = 31$, $p = 0.010$; glances: $U = 10$, $p < 0.001$). However, overall, more children were reported as having a privileged relationship with their cat (14/16) than with their dog (17/28) (Fisher's test: $p = 0.050$). This was especially true for ASD children (8/14 for dogs and 8/8 for cats; Fisher's test: $p = 0.040$), but less clear for TD children (9/14 for dogs and 6/8 for cats; Fisher's test: $p > 0.05$).

DISCUSSION

This study, where dog–child and cat–child spontaneous interactions were observed, shows clear differences in the visual attentional patterns according to the animal species involved: dogs showed more gazes toward children, whereas cats produced both gazes and glances equally. Mutual gazes were rare between children and cats. Children overall produced more gazes than glances toward the animals, whatever the species, and there was no correlation between the attention patterns of children and their pets. Only slight differences were observed according to the developmental status of children: TD children showed longer and more frequent gazes toward their cat than did ASD children. TD child–dog dyads were characterized by more gazes and TD child–cat dyads by more glances. ASD child–dog and ASD child–cat dyads did not differ in terms of attention structure. Overall, ASD children displayed much more visual attention

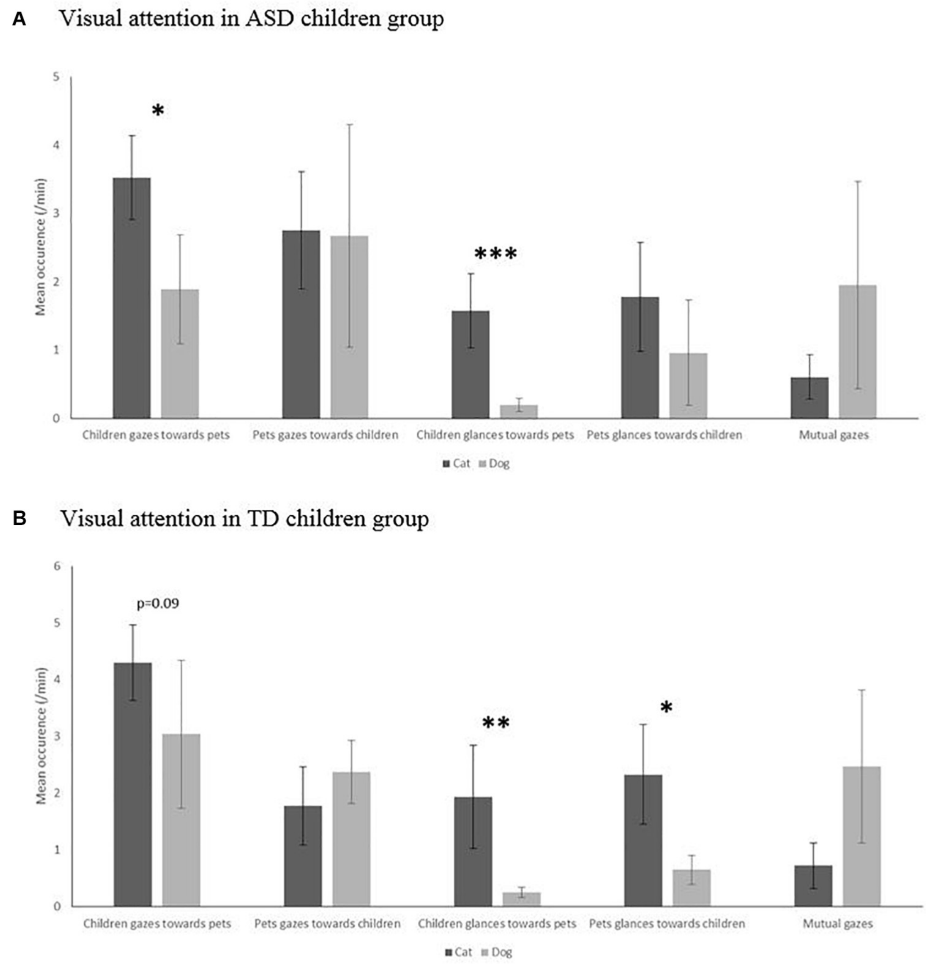

FIGURE 2 | Visual attention in occurrence per minute (glance, gaze, and mutual gaze) in cat–child dyads compared to dog–child dyads in the autism spectrum disorders (ASD) children group **(A)** and typically developing (TD) children group **(B)**. Mann–Whitney level of significance: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

with their pet cats than with their pet dogs and the same amount of visual attention toward their pets, whatever the species, as TD children. Interestingly, parents in both groups reported that their child had few visual interactions with cats as compared to parent reports of children with a dog. However, their reports indicated more bonding with cats than with dogs, especially in the ASD group.

These results confirm that species' intrinsic characteristics, probably as a result of long-term evolutionary processes, influence the pattern of visual attention in human–animal interactions. Dogs use more visual displays in intraspecific communication, attend to the group members' intentions through visual cues for social activities, which also allows coordination (Bradshaw and Nott, 1995). Visual communication is an important part of dogs' social lives, and the repertoire of visual signals is quite diversified, although it has been argued that, as a macrosmatic species, dogs would ignore visual information in some contexts (Szetei et al., 2003; Brucks et al., 2017). Here, our results, where dogs showed more prolonged gazes toward the child than did cats, would rather suggest that, in a pseudo-social context, visual attention is very important, as shown also in the context of intraspecific communication (e.g., Bradshaw and Nott, 1995; Call et al., 2003; Schwab and Huber, 2006; Nagasawa et al., 2015). It might be interesting to compare breeds with differential selections for olfactory skills, but our sample, here, based on opportunistic recruitment, would not allow such comparisons.

Cats, as solitary opportunistic gregarious animals, seem to not only have developed a less varied repertoire of visual signals but also rely less upon visual signals for communicating (Bradshaw and Cameron-Beaumont, 2000). Human children, on the other hand, as many primate species, showed an important pattern of visual attention through gazes toward their pets, although ASD children produced a comparatively more diversified profile. Interestingly, there was no real adjustment within the human–pet dyads and TD children kept showing long gazes to cats, although cats produced more glances than did dogs.

The important visual attention to their pets displayed by ASD children confirms the idea that pets are perceived as potential pseudo-social partners, being less intrusive and "judgmental" than humans. This also confirms that animal faces are less "aversive" than do human faces for these children (Grandin and Johnson, 2005; Grandgeorge et al., 2016). Interestingly, children and their cats were less often seen together than children with pet dogs (a third of the time of observation), which confirms the findings of Hart et al. (2018). Time spent together is also an indication of the type of interactions between the child and the pet (Hart et al., 2018). Despite that, parents indicate that more bonding occurred between the children and cats than dogs. This was especially true for the ASD group, confirming suggestions from Grandgeorge et al. (2012) and Hart et al. (2018) that cats are often more compatible companions.

Although some characteristics of cats, such as accepting being held, displaying "affectionate patterns," may, in some part, explain these results, there are large individual variations in such behaviors (Mertens, 1991; Hart et al., 2018), which means there may be other features of cats' behaviors that may explain this attractiveness, especially where ASD children are concerned. One possibility is that the visual attention pattern of cats, with more short glances and less sustained gazes than dogs, may also be more "comfortable" for these children. Recent studies have suggested (1) that direct gaze induces increased arousal in ASD children, this increase being correlated to the degree of social impairment (O'Haire et al., 2015; Kaartinen et al., 2016), and (2) that a less sustained visual attention toward ASD children allows them to be less inhibited and more of the "actor" in the relationship (Grandgeorge et al., 2017). The attention structure of cats, based on repeated glances, may be perceived as less "invasive" and, thus, more favorable for bonding than the long gazes of dogs, especially for ASD children.

Neither dogs nor cats showed a clear difference in their attentional behavior according to the child's developmental status, although their respective attention structures were more visible with TD children than with ASD children, suggesting some adjustments or modulations by human responses. Overall, the three species involved behaved in the interspecific interactions with their own species-specific visual attention patterning, dogs and TD humans performing more gazes overall during the interactions.

One limitation to this study was of course the length of the videos, which was determined by the ecological situation, but led to limited times of recordings, especially for the cats. Nevertheless, this was a representation of the child–pet relationships. However, this cannot be the sole explanation for the absence of a difference according to species for aspects like mutual gazes as the data, even on these limited samples, were very similar. Further researches should involve longer sampling and should also consider multimodal and complementary aspects of the interactions (e.g., tactile contact and vocal communication).

At that stage, these results strongly suggest, nevertheless, that interspecific interactions, even in the context of human–pet relationships, are highly dependent upon the evolutionary history of the species involved. Because humans rely a lot upon visual communication in their own social encounters, where direct gazes play a major role from early on, they may be especially sensitive to the gazing behavior of their dogs (Nagasawa et al., 2015). People with ASD, with a less typical pattern of interaction, may be more comfortable with the less "invasive" short glances of cats. Pet dogs and cats obviously "project" their own species-specific social skills in the human–animal situation. This means not only that interspecific communication has to be associated with processing and storing other species' ways of communicating in order to be successful (e.g., Hausberger et al., 2019) but also that the sensitivity to human cues, here the attentional state, demonstrated by different domestic and captive species, is, for a large part, the result of the species' own evolutionary history.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Restriction was asked by the participants. Requests to access these datasets should be directed to MG, marine.grandgeorge@univ-rennes1.fr.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. Ethical review and approval was not required for the animal study because data were collected between 2009 and 2012, in accordance with the (at that time) current French legislation. All dogs and cats involved in the study were family pets, hence under their owners' responsibility for care and use. The researchers had no involvement in any decision in this regard and the study was conducted in accordance with the French regulations governing the use of animals for research. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

MG and MH designed the experiment, contributed to the statistical analysis, and wrote the manuscript. MG organized the population recruitment. MG, HM, YG, and YB collected the data. MG, HM, YG, YB, and MH performed the analyses. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Talking to Cows: Reactions to Different Auditory Stimuli During Gentle Human-Animal Interactions

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The quality of the animal-human relationship and, consequently, the welfare of animals can be improved by gentle interactions such as stroking and talking. The perception of different stimuli during these interactions likely plays a key role in their emotional experience, but studies are scarce. During experiments, the standardization of verbal stimuli could be increased by using a recording. However, the use of a playback might influence the perception differently than "live" talking, which is closer to on-farm practice. Thus, we compared heifers' ($n = 28$) reactions to stroking while an experimenter was talking soothingly ("live") or while a recording of the experimenter talking soothingly was played ("playback"). Each animal was tested three times per condition and each trial comprised three phases: pre-stimulus, stimulus (stroking and talking) and post-stimulus. In both conditions, similar phrases with positive content were spoken calmly, using long low-pitched vowels. All tests were video recorded and analyzed for behaviors associated with different affective states. Effects on the heifers' cardiac parameters were assessed using analysis of heart rate variability. Independently of the auditory stimuli, longer durations of neck stretching occurred during stroking, supporting our hypothesis of a positive perception of stroking. Observation of ear positions revealed longer durations of the "back up" position and less ear flicking and changes of ear positions during stroking. The predicted decrease in HR during stroking was not confirmed; instead we found a slightly increased mean HR during stroking with a subsequent decrease in HR, which was stronger after stroking with live talking. In combination with differences in HRV parameters, our findings suggest that live talking might have been more pleasurable to the animals and had a stronger relaxing effect than "playback." The results regarding the effects of the degree of standardization of the stimulus on the variability of the data were inconclusive. We thus conclude that the use of recorded auditory stimuli to promote positive affective states during human-animal interactions in experimental settings is possible, but not necessarily preferable.

Keywords: cattle, animal welfare, human-animal communication, auditory perception, gentle talking, affective states, positive emotions, expressive behavior

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INTRODUCTION

The welfare of animals is strongly influenced by the animals' perception and evaluation of their environment and the affective reactions induced by it (Veissier and Boissy, 2007). Humans constitute a substantial part of their environment, especially in farm animals. The way animals perceive humans and the quality of their interactions has a strong impact on their welfare (Boivin et al., 2003; Waiblinger, 2019). How an interaction is perceived by an animal can be influenced by the behavior shown by the human: characteristics of movements, tactile interactions and the use of voice all contribute to whether an interaction is experienced positively, neutrally or negatively (Waiblinger, 2017). While the perception of tactile stimulation has been investigated in cattle (Schmied et al., 2008; Lange et al., 2020), less is known about the effects of vocal stimulation (Waiblinger, 2017). Despite possible benefits of applying auditory stimuli in farm environments (Waiblinger, 2019), research on the effects of gentle vocal interactions on farm animals is scarce.

Cattle have highly developed auditory abilities: their hearing ranges from 23 Hz to 37 kHz (Heffner, 1998). Vocalizations are an integral part of their intraspecific communication (Kiley, 1972; Watts and Stookey, 2000; Green et al., 2019); for instance, in an affiliative context, cows direct low-frequency calls toward their calves (Padilla de la Torre et al., 2016). But cattle are also responsive to human vocalizations: calves can learn to be called by individual names (Murphey and Moura Duarte, 1983) and cows learn to follow specific calls to go to the milking parlor (Albright et al., 1966). They also seem to be sensitive to characteristics of voice reflecting the human's affective state: heifers showed a clear preference for handlers talking gently compared to handlers shouting at them (Pajor et al., 2003); however, visual signals might have influenced their choice in this experiment.

Low-pitched vocal interactions with drawn-out vowels are considered part of positive, friendly milker behavior (Waiblinger et al., 2002; Ivemeyer et al., 2011). Both in practice (e.g., Waiblinger et al., 2003; Hanna et al., 2006) and in research (e.g., Rushen et al., 1999; Schütz et al., 2012), gentle interactions with cattle often include gentle tactile stimulation in combination with talking in a gentle, soothing voice. However, it is difficult to standardize talking in the context of scientific experiments without introducing artificiality by repeatedly using the same phrases. Using playback of recordings facilitates the repeated presentation of auditory stimuli and might be useful for simplification of experimental designs (Watts and Stookey, 2000). There is evidence that calves recognize recorded samples of their mother's calls (Barfield et al., 1994), and the playback of recorded calls of calves stimulated milk production in cows (Pollock and Hurnik, 1978; McCowan et al., 2002) and lowered their heart rate (Zipp et al., 2014). The playback of a recording of gentle talking over a loudspeaker could increase standardization while retaining a natural speech melody. However, there are no studies that investigated if the use of speakers is equally effective as talking directly to cattle, as the animals might perceive the vocal stimulus differently. Recorded speech differs in frequency composition, harmonics and resonance from speech generated directly by a human (Howard and Angus, 2006), and losses in lower and higher frequencies are visible in sonographic recordings of recorded compared to live spoken voice commands (Fukuzawa et al., 2005). Another difference might be the loss of multimodal information when the auditory stimulus is produced artificially and presented via the single channel of a playback, excluding other multimodal components (Watts and Stookey, 2000). Furthermore, if one single recording is used for multiple experimenters to achieve increased standardization, the resulting mismatch between the broadcasted voice and the individual experimenter might disturb the animal, since studies show that domestic animal species such as horses can form cross-modal representations about familiar human individuals (Proops and McComb, 2012). In addition, talking in a gentle voice might also change the handler's affective state and body language, as vocalization, breathing and posture are closely related to the quality of sound produced (Partan, 2013), and that way might influence the animals' perception of the interactions and the resulting affective state.

To investigate the effects of human-animal interactions on the affective states of animals, different behavioral and physiological parameters can be measured (Mendl et al., 2010). The valence of animals' affective experience can be evaluated by observing their behavior (Dawkins, 2015; Kremer et al., 2020), including their facial expressions (for a review see Descovich et al., 2017). During social licking (Sato et al., 1991; Laister et al., 2011) and stroking by humans (Schmied et al., 2008) cattle often show neck stretching, a behavior interpreted as indicative of a positive experience. Additionally, recent studies suggest that ear positions and movements can be helpful in the assessment of affective states in cattle (e.g., Lambert and Carder, 2019; Lange et al., 2020). Other indicators for affective states are cardiac parameters, e.g., the HR of heifers accelerated when exposed to recordings of human shouting (Waynert et al., 1999). Heart rate (HR) is regulated by sympathetic and parasympathetic activity. Heart rate variability (HRV) parameters reveal more detailed information about sympathovagal balance and thus allow investigation of internal states of animals (von Borell et al., 2007).

We compared heifers' reactions to stroking while an experimenter was talking soothingly ("live") or while a recording of an experimenter talking soothingly was played ("playback"). Even though earlier studies suggest that stroking in combination with auditory stimuli can elicit a positive, low-arousal state in cattle, this has not been shown for a stroking treatment with a playback auditory stimulus. We thus hypothesized that both forms of auditory stimulation in combination with stroking would lead to a positive, low-arousal state in the heifers; thus, we predicted a decrease of HR, an increase of HRV and an increase of behaviors indicating low arousal and positive valence. We expected some of these effects to last until shortly after stroking. Further, we hypothesized that live talking would elicit a more positive emotional state than talking played by a speaker. Finally, we hypothesized that the higher degree of standardization in the "playback" stimulus leads to lower variability in the data.

MATERIALS AND METHODS

Animals, Housing and Management

The experiment was discussed and approved by the institutional ethics committee in accordance with the Good Scientific Practice guidelines and national legislation (project number ETK-02/04/2017).

The study was performed with 28 heifers (27 Austrian Simmental, one Austrian Simmental × Brown Swiss) on the young stock farm of the University of Veterinary Medicine, Vienna (Rehgras, Furth an der Triesting, Austria) between May and November 2017. As we aimed to investigate positive emotions during human–animal interactions, a generally positive perception of close human contact was a prerequisite. Based on their positive animal-human relationship, we pre-selected 32 heifers. Twenty-eight of these animals were later used for the tests. The heifers' age ranged from 7 to 24 months. According to their age, two groups of 16 animals were formed. Housing, feed and general treatment was the same for both groups, which were kept mainly on pasture. Only during poor weather conditions and for testing the animals were brought into deep-litter pens with adjoining outdoor runs, where they were fed hay and concentrate. Water and mineral blocks were provided ad libitum.

The animals were carefully habituated to the camera (Sony HDR-CX730,Weybridge, UK) and HRV equipment (Polar Electro Oy, Kempele, Finland) as well as the experimenters (both female, green overalls; A: brown hair, 1.63 m; B: brown-reddish hair, 1.70 m), the loudspeakers (Denon Envaya mini$^{\text{TM}}$ DSB-100, Kawasaki, Japan; fixed to the strokers' chest, but not playing sound) and the stroking procedure, until it was possible to equip the free-moving heifers with the HRV girths and stroke the animals for 3 min without them walking away or showing any visible signs of unease. Animals were considered fully habituated when a full 9-min trial (see Section Experimental Procedure, no vocal stimulation) could be performed on them while they were lying without inducing any avoidance reactions. For further details of the selection and habituation process, see Lange et al. (2020).

Experimental Design

We applied a crossover design, i.e., each animal acted as its own control and was thus subjected to both treatments. To ensure robustness of the data, each animal experienced each treatment three times in an alternating pattern, i.e., in a total of six trials (trial numbers 1–6). Each trial consisted of three phases of 180 s (3 min) each: (1) pre-stimulus (PRE), where the experimenter stood next to the animal so that baseline values could be recorded; (2) stimulus (STIM), with the experimenter stroking the ventral neck while talking in a gentle voice ("live") or while a recording of the experimenter talking in a gentle voice was played ("playback"), and (3) post-stimulus (POST), where the experimenter was standing next to the animal again so that possible carry-over effects could be observed. Approximately half of the animals started with the "live" auditory stimulus, the other half with the "playback" stimulus. The experimenters aimed to balance the order of the treatments over each testing day, but complete balancing was not always possible.

Experimental Procedure

General Procedure

All trials were carried out in a deep-litter barn of 182 m^2 (min. 11 m^2/animal), which was familiar to all animals. Each animal was prepared and equipped for HRV measurement (POLAR® horse trainer transmitters and S810i monitors, Polar Elektro Oy, Kempele, Finland) by thoroughly wetting the coat and applying ultrasound gel at electrode sites, before using elastic girths to fix the electrodes and transmitters to the chest. The transmitters were protected by a second girth with a sewn-on pocket to contain the monitor. All trials were conducted on lying animals during resting phases to minimize the influence of physical activity on cardiac parameters. Before starting a trial, the handler (i.e., stroker) started a POLAR® monitor and placed it in the pocket of the girth. When an animal had been lying for at least 5 min, the camera operator assumed a position ∼2 m from the heifer with the camera approximately at the height of the heifer's eyes, filming the head/neck region from the heifer's left side with special focus on the left eye and ear. The stroker assumed a standing position next to the animal's left shoulder and started the trial. She wore rubber gloves with a rough surface and, when the STIM phase started, applied a constant, previously practiced pressure while stroking at a frequency of 40–60 strokes/min (Schmied et al., 2008). The loudspeaker was hanging around the strokers' neck and fixed to the stroker's chest. A trial was completed after 9 min or aborted earlier at the occurrence of an event likely to influence the animal's emotional or physiological state, e.g., standing up, falling asleep or social interactions (Lange et al., 2020). If a trial was stopped, the experimenters waited for at least 1 h before testing the animal again.

Auditory Stimuli

During the stimulus phase, all animals experienced tactile stimulation on the ventral neck as described in Lange et al. (2020). Additionally, they were exposed to different auditory stimuli. In the "live" condition, the stroker talked directly to the animals in a gentle voice as in previous studies (Lürzel et al., 2015b, 2016), using phrases with positive content (in German) that were spoken calmly, with long low-pitched vowels and a decrease in pitch toward the end of the words or phrases. For the "playback" condition, a sample of Experimenter A talking in a gentle voice in the same way as in the "live" condition was recorded in WAV format via a digital voice recorder (Linear PCM Recorder LS-3, Olympus, Japan). It was integrated into an audio file (see **Supplementary Data 1**) that was played via an MP3 player (SanDisk Clip Sport MP3 Player, SanDisk Corporation, Milpitas, USA) connected to the loudspeaker fixed to the strokers' chest. The volume of the loudspeaker was adapted (using the Smartphone Android App SoundMeter) to the volume of the experimenter talking before each sequence of trials, as the experimenter adjusted the volume of her voice to the surroundings (e.g., wind, farm work). We determined an average volume of 35–47 dB per day, while staying under a maximum level of 70 dB. To assess the acoustic qualities of our recording we used the free acoustic analysis software Praat (Boersma and Weenink, 2020). The mean pitch was

190.7 Hz (± 43.4 Hz standard deviation), which is lower than the mean pitch of a sample that was described as a soothing voice cue (236.2 Hz) in contrast to a harsh voice cue (322.1 Hz) (Heleski et al., 2015).

While the experimenter was stroking the animals continuously during the 3 min of the STIM phase, the vocal stimulus was only present in the first and last minute. In both conditions, spoken signals in the audio file announced the start and end of these 1-min periods as well as of the phases. Between the phases, there were 10-s breaks to allow the stroker to assume or leave the stroking position. Possible effects of the loudspeaker itself were thus present in both conditions and the auditory stimulus of the playback was as similar as possible to the "live" condition with respect to duration of speech. Two persons conducted the experiments; one stroked the animals, the other filmed the treatment. In two thirds of the trials the stroking treatment was performed by Experimenter A and in one third by Experimenter B, in a semi-randomized order.

Behavioral Observations

All trials were video recorded and the behavior was analyzed with the coding software Solomon Coder (version: beta 17.03.22, András Péter, Budapest, Hungary), using focal animal sampling and continuous recording (Martin and Bateson, 2007). The observer was blinded to the test condition as the head of the stroking person was covered on the screen during coding, so that possible lip movements were not visible. The observer recorded ear and head positions and movements as well as other behavior according to an ethogram (**Table 1**; for photographs of ear positions, see **Supplementary Figures 1**, **2**). To determine the intra-observer reliability, ten 2-min video sequences were chosen from videos not used for further analyses and coded twice. Cohen's kappa for ear postures was 0.61, for eye aperture 0.63 and for the head postures 0.71. Cohen's kappa for rumination and lying position was 1 and for miscellaneous behaviors 0.64.

Heart Rate Measurements

Inter-beat intervals were error-corrected and processed according to Hagen et al. (2005) using the Polar Precision Performance Software, version 4.03.050 (Polar Electro Oy, Kempele, Finland), and HR and HRV parameters were calculated using Kubios, version 2.0 (Biosignal Analysis and Medical Imaging Group, Department of Applied Physics, University of Eastern Finland, Kuopio, Finland). To account for the respiratory rate, frequency bands were set to 0.04–0.2 Hz for the low frequency band and 0.2–0.58 Hz for the high frequency band (von Borell et al., 2007). The following parameters were analyzed statistically: mean heart rate (*HR*); time domain: standard deviation of the inter-beat intervals (*SDNN*) and square root of the mean squared differences of successive inter-beat intervals (*RMSSD*), and the ratio of *RMSSD* and *SDNN* (*RMSSD*/*SDNN*); frequency domain (using fast Fourier transform): normalized powers of high (*HF*) and low frequency (*LF*), and the ratio of *LF* and *HF* (*LF*/*HF*).

Statistical Analysis

Behavioral Data

We used the software package R, version 3.5.2 (R Core Team, 2019). The durations of behaviors that occurred often enough to be suitable for analysis were transformed to proportions by dividing them by the total time during which they could be observed. To account for the fact that the ear positions are mutually exclusive and their proportions always amount to one, we tried to fit a compositional model but the large amount of zeros led to convergence problems. Therefore, we selected the three ear positions that were observed often enough for statistical analysis. They were analyzed using generalized linear mixed models (GLMMs) (Baayen, 2008) with a beta error structure and logit link function (McCullagh and Nelder, 1989; Bolker, 2008) using the package "glmmTMB," version 0.2.3 (Brooks et al., 2017). Because values of the responses being exactly 0 or 1 can lead to infinite point probabilities in beta distributions, the response variables were transformed according to $(y \times (n - 1) + 0.5)/n$, where y is the original response and n the number of observations (Smithson and Verkuilen, 2006), resulting in regular small shifts of the values away from 0 and 1 (e.g., for $n = 534$, 0 becomes 0.00094, 1 becomes 0.99906).

Ear hanging and the other downward ear positions did not occur often enough to be evaluated statistically on their own [median duration in s (min–max): *hanging* 0 (0–155)]. Thus, we calculated the variable *low ear* by summing up the durations of downward ear positions (*hanging* + *back down* + *center down* + *forward down*; summed up to *low*). The result of *low ear* was still dominated by zeros, causing difficulties with the beta error distribution; therefore, it was dichotomized (occurrence: yes/no) and analyzed using a GLMM with a binomial structure and logit link function. The behavior *changes of ear position* was calculated by summarizing the frequency of different ear positions and subtracting 1 (for the initial ear position), and analyzed using a GLMM based on the negative-binomial distribution with a log link function. A minimum of three observations per condition per animal were included in statistical analyses. If additional tests were performed due to technical problems in HR(V) data collection, up to four tests per condition could be included (9 cases), which resulted in a sample size for models of 534 measures in total made for 28 individuals in a total of 178 trials with 3 phases each. For all full models, fixed effects were treatment (factor with two levels: live, playback), phase (factor with three levels: PRE, STIM, POST) and their interaction, and individual as well as trial ID (trial number nested in individual) as random effects. Trial ID was included as a random effect to account for the fact that each trial consisted of three phases and thus contributed three data points, where it seemed plausible to assume that there was random variation between the trials. We included random slopes within individual for trial number (to account for possible changes caused by treatment repetition), treatment and phase to allow their effects to vary between individuals (Barr et al., 2013). To address the issue of cryptic multiple testing (Forstmeier and Schielzeth, 2011), we compared each full model with a respective null model that lacked the variables of interest (phase and the interaction of phase and treatment) but was otherwise identical. We used a likelihood ratio test (R

TABLE 1 | Ethogram (Lange et al., 2020).

Category	Behavior[a]	Definition
Inactive ear posture[b]	Ear hanging	The ear loosely hangs downwards (referring to the ground). There is no visible muscle tension, leading often to a slightly bouncing movement when the position is assumed.
Active ear postures[b,c]	Back up	The ear is held behind and above the latero-lateral axis.
	Back center	The ear is held behind and at the same height as the latero-lateral axis.
	Back down	The ear is held behind and below the latero-lateral axis.
	Center up	The ear is held perpendicular to the head and above the latero-lateral axis.
	Center	The ear is held perpendicular to the head along the latero-lateral axis.
	Center down	The ear is held perpendicular to the head and below the latero-lateral axis.
	Forward up	The ear is held in front of and above the latero-lateral axis.
	Forward center	The ear is held in front of and at the same height as the latero-lateral axis.
	Forward down	The ear is held in front of and below the latero-lateral axis.
	Ear flicking	The ear is quickly (within max. 0.5 s) moved back and forth at least once. The behavior is coded until one of the other ear postures is clearly visible again. The residual movement after the active movement is still part of ear flicking.
Head/neck postures	Held without touching	The head is actively held up and does not touch the stroker.
	Held with touching	The head is actively held up and touches the stroker.
	Rest head without touching	The heifer does not actively carry the head's weight. The heifer's head is in contact with the ground, barn equipment, another animal or with the heifer's leg(s). The heifer's head is not in contact with the stroker.
	Rest head with touching	The heifer does not actively carry the head's weight. The heifer's head is lying on the ground, barn equipment, another animal or the heifer's leg(s) while being in contact with the stroker, or it is lying on the stroker's leg.
	Head shaking/tossing	Successive quick movements of the head. The movements can be rotational or up and down.
	Neck stretching	Positioning neck and head actively in an outstretched line, either up, down, or forward.
Eyes[d]	Open	The iris is at least partly visible.
	Closed	The iris is not visible at all for longer than 0.5 s.
	Not visible	Neither eye is visible.
Miscellaneous	Rubbing the stroker	The heifer touches the stroker and moves the touching body part while in contact with the experimenter. The behavior ends when the contact between the heifer and the person is interrupted for at least 3 s.
	Rubbing	The heifer moves the head/neck region while in contact with the ground or barn equipment. The behavior ends when the contact between the heifer's head/neck region and the ground/equipment has ended.
	Nose close	The heifer moves her muzzle toward the stroker within a range of 5 cm. The behavior ends when the heifer's nose does not point toward the stroker anymore, leaves the range of 5 cm or if another behavior of the "miscellaneous" category starts.
	Licking the stroker	The heifer's tongue touches the stroker at least once. The behavior ends when the heifer's tongue does not touch the stroker again within 3 s.
	Ruminating	The heifer's jaw moves regularly sideways with a frequency of about one movement per second. This movement is recorded as rumination if it occurs in a series of at least five movements (which may start before and end after the observation). Rumination ends when the jaw movement is paused for more than 10 s.
Calculated measures	Contact	The time in which the heifer's head and neck area was in contact with the stroker. Sum of durations of "rest head with touching", "held with touching", "nose close", "rubbing experimenter" and "licking experimenter", not including contact established by stroking.
	Resting head	Sum of durations of "rest head with touching" and "rest head without touching".
	Ear low	The sum of the durations of the ear hanging or held below the latero-lateral axis ("hanging" + "back down" + "center down" + "forward down").
	Changes of ear positions	Sum of the frequencies of different ear positions per trial minus 1.

[a] *All behaviors were coded as durations, except changes of ear positions (count data).*

[b] *The left ear was recorded; if it was not visible, the right ear was recorded.*

[c] *The latero-lateral axis refers to an imaginary line between the bases of the ears. "Behind" means the ear is pointing toward the back of the head, "in front" refers to the rostral end of the head, "above" describes the ear pointing dorsally and "below" pointing ventrally. If the observed ear was moved by the experimenter, the position before the movement was recorded until the next unambiguous ear posture was assumed.*

[d] *The left eye was recorded; if it was not visible, the right eye was recorded.*

function "anova") for these comparisons. The significance of the individual independent variables was determined by dropping them one at a time and using a likelihood ratio test to compare the resulting models to the full model (Barr et al., 2013). Values of $p \leq 0.05$ are referred to as significant, and $0.05 < p \leq 0.1$ as a trend (Stoehr, 1999). If the full–null model comparison was, or tended to be, significant and the interaction was non-significant, the interactions were removed from the models and reduced models were fitted to investigate the main effect of phase. Main effects of treatment were not tested, as they were not of interest.

As stated above, the mismatch between the broadcasted voice and the individual experimenter stroking the animal, as was the case when experimenter B was stroking during the playback of the voice of experimenter A, could drive the results regarding the interaction between condition and phase. If this were the case, one would expect the pattern of this interaction to depend on whether the mismatch was present or not. To address this question, we fitted one model in addition to each full model. This model included the three-way interaction between phase, treatment and presence of the mismatch and all terms comprised therein (and a random slope of presence of the mismatch), but was otherwise identical to the respective full model. Subsequently, we compared this model to a reduced model lacking the three-way-interaction but otherwise being identical, again using a likelihood ratio test (R function "anova"). If this comparison reveals significance, it indicates that the effects of condition and phase were indeed driven by the mismatch. In the case of the model for the behavior *neck stretching*, the reduced model did not converge, but we inspected the coefficients of the full model to reveal possible effects of the mismatched experimenter/voice combination on the duration of *neck stretching*. We found no evidence for significant effects of the mismatch between the broadcasted voice and the individual experimenter stroking the animal for any of the behaviors (*neck stretching* $z = 0.534$, $p = 0.593$ (full model coefficients); *contact* $\chi^2 = 0.223$, df = 2, $p = 0.895$; *eye closed* $\chi^2 = 0.025$, df = 2, $p = 0.988$; *head resting* $\chi^2 = 0.451$, df = 2, $p = 0.798$; *ear flicking* $\chi^2 = 0.916$, df = 2, $p = 0.632$; *changes of ear position* $\chi^2 = 0.522$, df = 2, $p = 0.770$; *back up* $\chi^2 = 0.077$, df = 2, $p = 0.962$; *back center* $\chi^2 = 2.746$, df = $p = 0.253$; *forward up* $\chi^2 = 0.937$, df = 2, $p = 0.626$; *ear low* $\chi^2 = 0.684$, df = 2, $p = 0.710$). Hence, we report results of the models not including the mismatch.

Since the "playback" stimulus had a higher degree of standardization than the "live" stimulus, it seemed plausible that the variation in a given behavior would be smaller in the "playback" treatment than in the "live" treatment. We explicitly estimated this potential effect by modeling the precision parameter of the response as a function of treatment in each model (Lange et al., 2020). With a higher degree of standardization in "playback" stroking, we expected smaller variation in behaviors, and thus, larger estimated precision parameters. For the models where we found overdispersion (*neck stretching*, *changes of ear positions, contact, head resting* and *forward up*), we corrected standard errors and *p*-values based on Wald's z-approximation (Field, 2005); therefore no degrees of freedom are reported and χ^2s were replaced by z-values (Gelman and Hill, 2006). We determined 95% confidence limits using the function "simulate.glmmTMB" of the "glmmTMB" package. We assessed the model stability by comparing the estimates of models based on the full dataset with estimates of models fitted to subsets where the levels of each random effect were dropped one at a time (Nieuwenhuis et al., 2012). This revealed a fairly good stability of the models.

For graphical depiction, we used the R packages "ggplot2" (Wickham, 2016) and "cowplot" (Wilke, 2019). Data were depicted as boxplots for each treatment and phase, using the mean values of behaviors per animal (averaged across the three trials per treatment). The bold line corresponds to the median; the lower and upper lines of the box to the first and third quartile, respectively; and the whiskers correspond to the lowest and highest values that were still within 1.5 × interquartile range from the margins of the box. Outliers (all values outside of 1.5 × interquartile range) are depicted as circles.

Cardiac Data

Due to technical problems during HRV recording (i.e., >5% of errors per minute), we obtained a sample size of 26 animals, which resulted in 176 total measures as sample size for models. Because of an insufficient number of recordings with experimenter B, only recordings of tests where experimenter A stroked the animals were used for HRV analysis. Cardiac variables were analyzed using linear mixed models (LMMs) with the package "lme4" (Bates et al., 2015), including treatment, phase and their interaction, age (d), time of day, *HR* (unless it was the response variable) and duration of rumination (s) as fixed effects. Heart rate was included as a fixed effect because it is often strongly correlated to HRV indicators (Zaza and Lombardi, 2001; Monfredi et al., 2014; Sacha, 2014; McCraty and Shaffer, 2015). While HR is often regarded as an indicator of arousal (Zebunke et al., 2013; Briefer et al., 2015; Travain et al., 2016; Lambert and Carder, 2019), HRV might also provide information on valence (Boissy et al., 2007). By correcting for *HR* in the models, the results represent the influence of the other independent variables (mainly the interaction of treatment and phase) on HRV parameters independently of their influence on *HR*, allowing conclusions in addition to those that can be drawn from *HR*. To account for the cyclical nature of circadian rhythms that influence HRV (Hagen et al., 2005; Kovács et al., 2016), we modeled time of day turning time into radians: first we transformed time to decimal numbers by summarizing hours, minutes divided by 60 and seconds divided by 3,600. The result was multiplied with $2 \times \pi$ and divided by 24, and the resulting variable was included together with its sine and cosine into the model (Stolwijk et al., 1999). The individual and trial number nested in individual were considered as random effects. We included random intercepts and random slopes within individual for trial number (to account for possible effects of treatment repetition), treatment and phase to allow their effects to vary between individuals. Where possible, we also included estimates of the correlations between the random intercept and slopes into the model (Barr et al., 2013). However, for the response variables *SDNN* and *LF*, the models including the correlations did not converge and we dropped the correlation estimates from

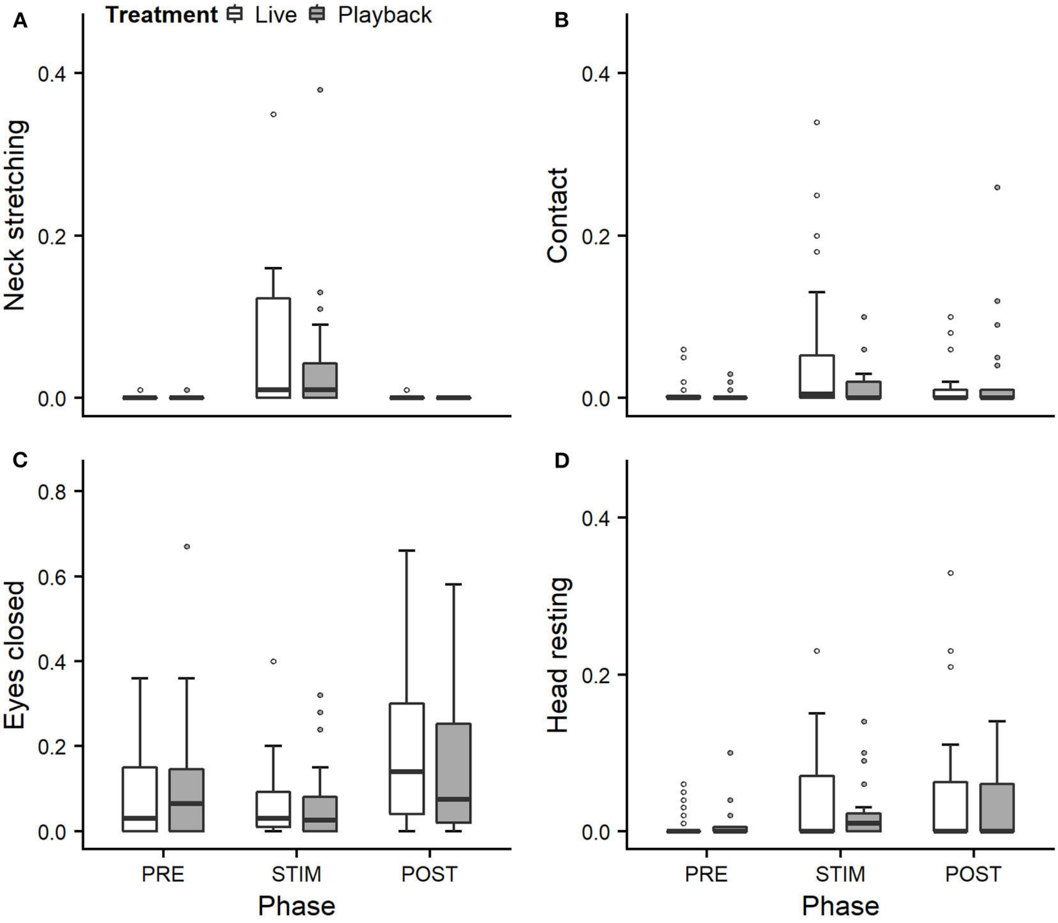

FIGURE 1 | Mean durations (as a proportion of the total time observed) of *neck stretching* **(A)**, *contact* **(B)**, *eyes closed* **(C)**, and *head resting* **(D)** of heifers ($n = 28$) during the experimental trials. Means were calculated across the three trials per treatment and are depicted according to the treatment used (white = "live," dark gray = "playback") and phase (PRE = pre-stimulus, STIM = stimulus, POST = post-stimulus). Statistics for GLMMs: significant main effect of phase for *neck stretching* **(A)**, $p < 0.05$. Note that the y-axis scale varies to allow for sufficient resolution for rare behaviors.

the model. We then proceeded in the same way as described above: we fitted a null model that lacked the variables of interest (phase and the interaction of phase and treatment), and if the full-null model comparison revealed significant differences and the interaction was non-significant, it was removed from the model and reduced models were fitted to test for the significance of the main effect of phase.

RESULTS

Behavior During Gentle Interactions

We statistically analyzed *neck stretching* (median duration in s; min–max: 0; 0–112), *contact* (0; 0–175), *eye closed* (0; 0–180) and *head resting* (0; 0–180) (**Figure 1**); the ear positions *back up* (124; 0–180), *back center* (8; 0–180), *forward up* (0; 0–164), *ear low* (0; 0–169); and the ear movements *ear flicking* (1; 0–76) and *changes of ear position* (9; 0–63) (**Figure 2**).

Full and null models differed significantly for the response variables *neck stretching* (**Figure 1**; GLMM: $\chi^2 = 10.811$, df = 4, $p = 0.029$), *ear flicking* (**Figure 2**; $\chi^2 = 32.426$, df = 4, $p < 0.001$) and *changes of ear position* (**Figure 2**; $\chi^2 = 35.907$, df = 4, $p < 0.001$) as well as for all the tested ear positions except for *forward up* (**Figure 2**; *back up*: $\chi^2 = 31.371$, df = 4, $p < 0.001$; *back center*: $\chi^2 = 13.613$, df = 4, $p = 0.009$; *ear low*: $\chi^2 = 19.758$, df = 4, $p = 0.001$). The full–null model comparisons revealed a statistical tendency toward a difference for *forward up* (**Figure 2**; $\chi^2 = 9.332$, df = 4, $p = 0.053$) and no significant difference for *contact* (**Figure 1**; $\chi^2 = 2.067$, df = 4, $p = 0.723$), *head resting* (**Figure 1**; $\chi^2 = 2.024$, df = 4, $p = 0.731$) and *eyes closed* (**Figure 1**; $\chi^2 = 6.113$, df = 4, $p = 0.191$).

As the interaction of phase and treatment was not significant for any of the behaviors we analyzed, effects of the phase were not influenced by the type of auditory stimulus used in the treatment. However, independently of which treatment was used, the phase had a significant effect on several of the behaviors. The reduced models revealed a significant main effect of phase for *neck stretching* ($z = 2.594$, $p = 0.009$), *ear flicking* ($\chi^2 = 32.520$, df = 2, $p < 0.001$) and *changes of ear position* ($\chi^2 = 31.526$, df = 2, $p < 0.001$): while the durations of *neck stretching* increased during STIM (**Figure 1**), the durations of

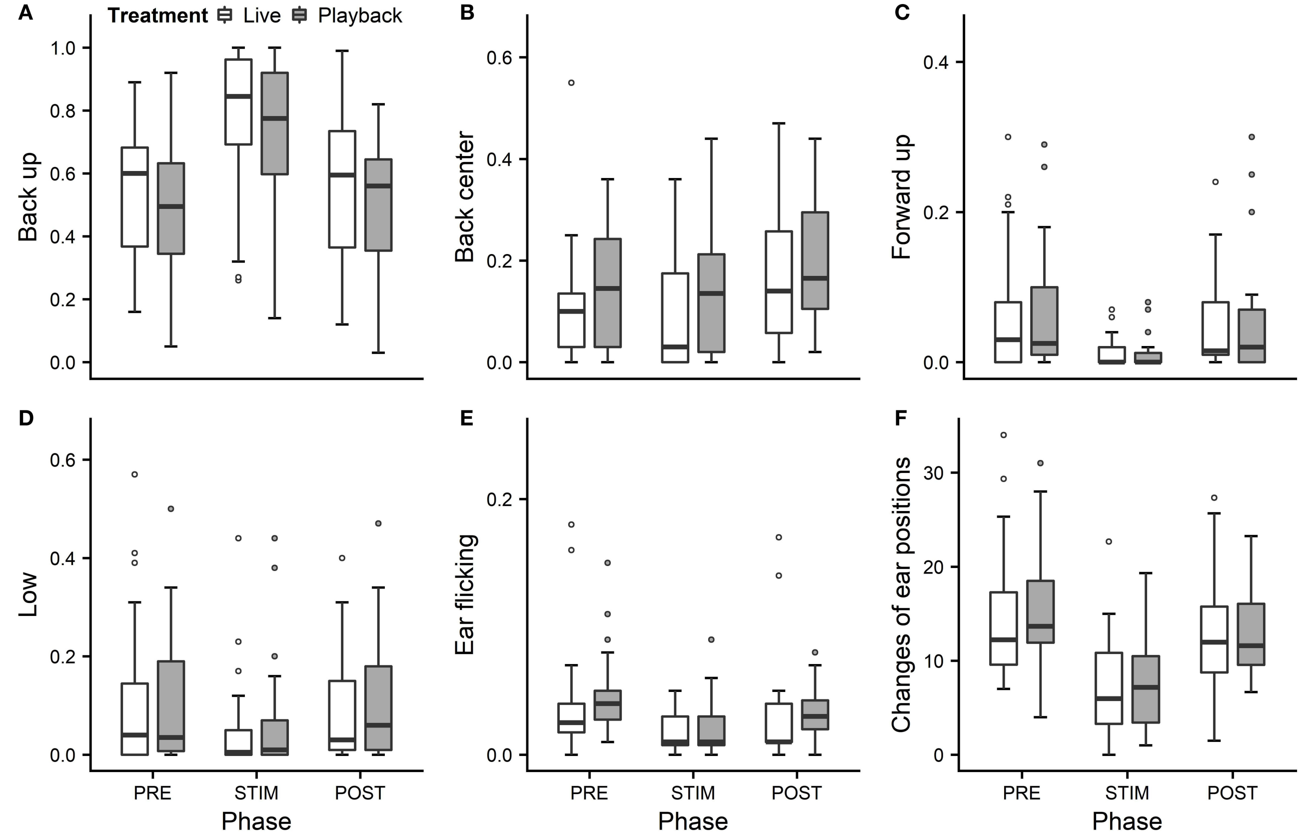

FIGURE 2 | Mean durations of ear positions **(A–D)** and ear flicking **(E)** as a proportion of the total time observed and **(F)** mean number of changes of ear positions of heifers (n = 28) during the experimental trials. Means were calculated across the three trials per treatment and are depicted according to the treatment used (white = "live," dark gray = "playback") and phase (PRE = pre-stimulus, STIM = stimulus, POST = post-stimulus). Statistics for GLMMs: significant main effect of phase for *back up* **(A)**, *back center* **(B)**, *ear low* **(D)**, *ear flicking* **(E)**, and *changes of ear positions* **(F)**, $p < 0.05$; and trend for *forward up* **(C)**, $p < 0.1$. Note that the y-axis scale varies to allow for sufficient resolution for rare behaviors.

ear flicking and the numbers of *changes of ear position* decreased (**Figure 2**). Phase also had a significant effect on the ear positions *back up* (χ^2 = 30.705, df = 2, $p < 0.001$), *back center* (χ^2 = 13.500, df = 2, p = 0.001), *forward up* ($z = -0.216$, p = 0.027), and *ear low* (χ^2 = 19.094, df = 2, $p < 0.001$): during STIM, the durations of *back up* increased significantly, whereas the durations of the other tested ear positions decreased (**Figure 2**).

The variability was significantly smaller in the "playback" treatment for *neck stretching* (χ^2 = 16.177, df = 1, $p < 0.001$) and *contact* (χ^2 = 4.321, df = 1, $p < 0.001$), but higher for the ear position *back center* (χ^2 = 10.273, df = 1, $p <$ 0.001). It did not differ significantly for the other behaviors. For statistical details, including model coefficients, standard errors and confidence intervals, see Supplementary Material (**Supplementary Table 1**).

The number of tests aborted because of heifers standing up during STR without any obvious reason (e.g., being chased up) was higher in the "playback" condition (n = 13) than the "live" condition (n = 6) but did not differ significantly (χ^2 = 2.3, df = 1, p = 0.127).

Cardiac Data

Full and null models differed significantly for the response variables *HR* (LMM: *HR*: χ^2 = 26.688, df = 4, $p < 0.001$), *SDNN* (χ^2 = 13.185, df = 4, p = 0.010), *RMSSD*/*SDNN* (χ^2 = 13.091, df = 4, p = 0.011) and *HF* (χ^2 = 12.272, df = 4, p = 0.015). The full–null model comparison revealed no significant difference for *RMSSD* (χ^2 = 2.933, df = 4, p = 0.569), *LF* (χ^2 = 0.645, df = 4, p = 0.958) and *LF*/*HF* (χ^2 = 2.784, df = 4, p = 0.595).

The interaction of phase and treatment was significant for all cardiac parameters with a significant full-null model comparison (**Supplementary Table 2**, *HR*: χ^2 = 9.917, df = 2, p = 0.007; *SDNN*: χ^2 = 8.738, df = 2, p = 0.013; *HF*: χ^2 = 7.657, df = 2, p = 0.022; *RMSSD*/*SDNN*: χ^2 = 8.378, df = 2, p = 0.015). Whereas *HR* increased slightly during stroking in both conditions, it decreased more strongly in the "live" condition after the treatment (**Figure 3**). There was a distinct increase in SDNN during STIM in the "live" condition, followed by a decrease in POST, whereas the strongest increase in the "playback" condition took place in POST. *RMSSD*/*SDNN* mirrored this pattern: in "live" it decreased during STIM, increasing again in POST, and in "playback" it decreased during POST. *HF* increased by nearly

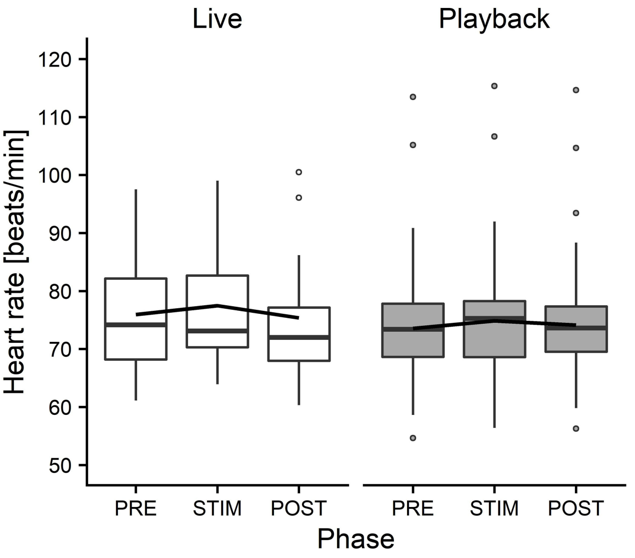

FIGURE 3 | Means of heart rate of heifers ($n = 26$), calculated across the three trials per treatment and depicted according to treatment (white = "live," gray = "playback") and phase (PRE = pre-stimulus, STIM = stimulus, POST = post-stimulus). The black line indicates the estimated means of the models. Statistics for LMM: significant interaction of condition and phase, $p < 0.05$.

30% during POST of the "live" condition whereas it decreased during POST in "playback" (**Figure 4**). The models revealed a significant negative effect of *HR* on all the HRV parameters except *LF* and *LF/HF*, where it had a significant positive effect (see **Supplementary Table 2**).

DISCUSSION

We compared the reactions of heifers to stroking while applying two different auditory stimuli: the stroker talking directly to the animals in a gentle voice or a recording of the stroker's talking. We found behavioral and physiological indications of a positive perception of the interactions for both auditory stimuli. While the behavioral reactions to gentle interactions did not differ statistically, some of the cardiac parameters indicated differences between the auditory stimuli, also shortly after the presentation of the stimulus had ended.

Perception of Each Treatment

Both treatments led to changes in behavior during the STIM phase that indicate a positive perception: During stroking, the heifers showed significantly longer durations of *neck stretching*, a behavior shown during intraspecific social grooming (Sambraus, 1969; Reinhardt et al., 1986; Schmied et al., 2005), which is often actively solicited, and stroking by humans (Waiblinger et al., 2004; Schmied et al., 2008; Lürzel et al., 2015a). It is interpreted a sign of enjoyment, and it can thus be assumed that the situation is perceived as positive.

In a previous, similar experiment (Lange et al., 2020), we observed decreases of *ear flicking* and *changes of ear position* during stroking with no auditory stimuli. The present study confirms this pattern. The animals showed less *ear flicking* during STIM than PRE, a behavior mostly associated with negative affective states, such as pain after dehorning (Heinrich et al., 2010; Neave et al., 2013) or reactions to insect attacks (Mooring et al., 2007).

During STIM, the animals also changed the positions of their ears less often than in PRE. Frequencies of *changes of ear positions* were lower in sheep feeding (Reefmann et al., 2009a) or voluntarily being groomed by a human (Reefmann et al., 2009b) than during separation from the herd. In contrast, dairy cows showed an increased frequency of *changes of ear positions* during stroking compared to before or after (Proctor and Carder, 2014), which might however have been caused by small differences in experimental design, such as the stroker approaching at the beginning of the stroking phase. In contrast, the decrease in *changes of ear positions* and *ear flicking* during stroking in the current as well as in our previous study (Lange et al., 2020) indicates an association of a reduction of these behaviors with a positive, low-arousal state also in cattle.

However, for some of the behaviors we expected to indicate affective states, the treatment did not lead to significant differences: previously observed effects of stroking (Lange et al., 2020) on the duration of the animal *resting* its *head* and the time spent in *contact* with the experimenter were not confirmed in this study. These findings might be connected with the auditory stimulus, which might keep the animal comparatively more attentive to a certain degree and thus limit the intensity of the relaxation.

In an attempt to reflect the continuous nature of ear positions, we recorded nine different positions along the vertical and the horizontal axis: *back up, back center, back down, center up, center, center down, forward up, forward center* and *forward down*, plus *ear hanging*. During stroking, durations of the *back up* position increased significantly, while durations of *forward up* and *ear low* decreased, mostly in line with our previous experiment (Lange et al., 2020). The tendency toward decreased durations of *forward up* might indicate lowered vigilance (Boissy and Dumont, 2002), which is associated with less fear (Welp et al., 2004), and could corroborate the hypothesis that stroking induces positive low-arousal states.

We predicted to find longer durations of *ear low* during stroking, because *low ear* positions, including *ear hanging*, were associated with low-arousal, positive affective states in dairy cows in previous studies (Schmied et al., 2008; Proctor and Carder, 2014). However, we observed predominantly *back up* positions and surprisingly rare occurrences of *ear low*. One possible reason might have been the strokers' position kneeling next to the lying animal and resulting in the auditory signal being located above and behind the heifers' ears in both conditions. Since the ear position pattern was very similar to the one found in our previous study without vocal stimulation (Lange et al., 2020), however, the effect of the auditory stimulus seems not to have had a strong influence on ear positions, possibly

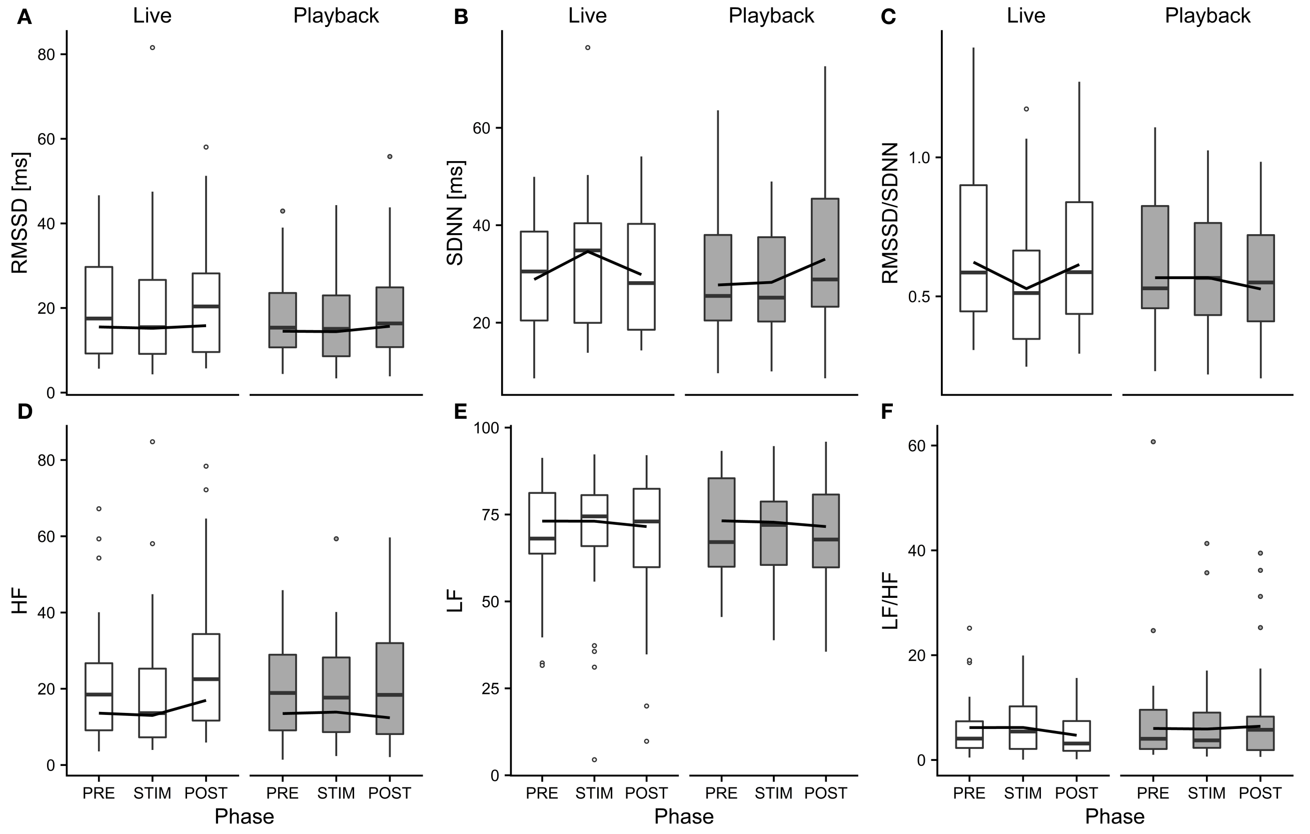

FIGURE 4 | Means of heart rate variability parameters *RMSSD* **(A)**, *SDNN* **(B)**, *RMSSD/SDNN* **(C)**, *HF* **(D)**, *LF* **(E)**, and LF/*HF* **(F)** of heifers ($n = 26$), calculated across the three trials per treatment and depicted according to treatment (white = "live," gray = "playback") and phase (PRE = pre-stimulus, STIM = stimulus, POST = post-stimulus). The black line indicates the estimated means of the models. Statistics for LMMs: significant interaction of condition and phase for *SDNN* **(B)**, *RMSSD/SDNN* **(C)**, *HF* **(D)**, $p < 0.05$.

because cattle have a relatively low sound-localization acuity compared with other mammals (Heffner and Heffner, 1992); the stroker's position relative to the animal's head may nevertheless be relevant.

Furthermore, the effects that we saw in STIM were not observed in POST, contrary to our hypothesis of longer-lasting effects of the treatment on behavior. However, some of the observed behaviors (such as *neck stretching* and the different ear positions) are more immediate reactions to positive stimuli and do not allow to observe longer-lasting changes in affective states.

Comparison of the Treatments

As there were no significant differences in the behavioral reactions to the two different auditory stimuli, stroking and talking in a gentle voice *per se* seem to have a stronger effect on the behavior than the source of the auditory stimulus. As this experiment did not include a treatment where the animals were stroked without any auditory stimulation, we cannot infer any information on whether gentle talking in general enhances or diminishes the positive effects of stroking, but the results are very similar to our previous study, where the animals were stroked without acoustic stimulation. Stroking can elicit quite strong effects on physiology and behavior in different species (rats: Holst et al., 2005; cows: Schmied et al., 2010; cats: Gourkow et al., 2014; lambs: Coulon et al., 2015; horses: Lansade et al., 2018), which might exceed possible consequences of small differences in auditory stimuli. Regarding the absence of significant differences in behavior, it seems plausible that the heifers did not discern the two auditory stimuli, at least not to an extent where it would have affected their behavior. Furthermore, the mismatch of experimenter and playback voice did not have a significant effect on any of the behaviors. Indeed, there is a substantial amount of literature in different species indicating that they do not necessarily distinguish playback from live auditory stimuli: playback is used successfully in studies investigating bird behavior (Douglas and Mennill, 2010), dogs react to dog-directed human speech played back from a loudspeaker (Ben-Aderet et al., 2017; Benjamin and Slocombe, 2018), and dairy cows increase their production when exposed to a playback of calf vocalizations (Pollock and Hurnik, 1978; McCowan et al., 2002; no effect if calves are reared with their mothers: Zipp et al., 2013). Other characteristics of speech might thus have a stronger impact on the animals' behavior than the characteristics induced by the type of source.

On the other hand, the analysis of cardiac parameters points toward a different perception of the two auditory stimuli. In both conditions, *HR* increased from PRE to STIM and decreased from STIM to POST, but this decrease was significantly more pronounced in the "live" condition, indicating a stronger relaxation effect of live talking after the presentation of the stimulus. The slight increase of *HR* during STIM in both conditions seems to contradict our expectation that our treatment would induce a low-arousal state. However, it is in line with previous findings reporting an increased *HR* of lying animals that were licked by conspecifics (Laister et al., 2011) or receiving a stroking treatment (Lange et al., 2020) and might be caused by physical reactions to stroking (e.g., *neck stretching*) more than by a meaningful change in arousal or affective state (Lange et al., 2020).

Independently of the changes in *HR*, there were some significant effects of the conditions on HRV parameters: *HF* increased in POST in the "live" condition, but decreased in POST in the "playback" condition. It is widely accepted that *HF* increases with increasing activity of the parasympathetic branch of the autonomic nervous system (Task Force of ESP and NASPE, 1996; von Borell et al., 2007). The increased values suggest a higher parasympathetic activity after stroking in the "live," but not the "playback" condition. An increased *HF* may be associated with positive emotions (McCraty et al., 1995; von Borell et al., 2007) and was found in horses regularly receiving a relaxing massage (Kowalik et al., 2017). This increase in *HF* was not accompanied by an increase in *RMSSD*, although both represent vagal activity and are often correlated (Task Force of ESP and NASPE, 1996; Hagen et al., 2005; von Borell et al., 2007; Shaffer et al., 2014). However, changes in *RMSSD* were not consistently observed in other studies investigating different affective states in animals (Reefmann et al., 2012; Travain et al., 2016). *RMSSD* might therefore be a suboptimal indicator of animal affective states (Gygax et al., 2013; Tamioso et al., 2018). A different pattern emerged for *SDNN*: values increased from PRE to STIM in the "live" condition, and decreased again in POST, whereas in the "playback" condition, *SDNN* reached its highest values in POST. *SDNN* reflects influences of both parasympathetic and sympathetic activity (von Borell et al., 2007; Shaffer et al., 2014). Together with the decrease of *RMSSD/SDNN* during live talking, these findings might indicate that the "live" condition led to higher sympathetic activity during stroking and talking, possibly indicating positive arousal in response to being stroked (Tamioso et al., 2018). The increase of *RMSSD/SDNN* in "live" in POST is in line with increased values observed in sheep being brushed by a familiar human (Tamioso et al., 2018), and, in combination with the observed increase of *HF* in POST in "live," indicates a shift toward vagal dominance after live talking. These patterns were not observed in the "playback" condition; contrarily, *SDNN* increased in POST, while *RMSSD/SDNN* and *HF* decreased slightly, possibly indicating a relative shift towards sympathetic regulation after stroking with "playback" stimulation.

In combination, the HRV results suggest that live talking may have been more pleasurable to the animals than "playback" and led to increased parasympathetic activity in the POST phase. They thus support the interpretation of a more pronounced relaxation effect indicated by the stronger decrease of *HR* in POST in "live" than in "playback." The difference between the two auditory stimuli might be caused by losses of lower and higher frequencies of recorded sound, which have been found to cause a decline in dog's responses to commands, especially in the absence of certain non-verbal cues (Fukuzawa et al., 2005). As we could not measure the actual sound pressure reaching the animals' ears directly, we can neither exclude the possibility that there might have been other systematic differences between the acoustic signals produced by two sources, such as consistent differences in volume, which might have contributed to eliciting higher or lower arousal. Another difference between the situations might have been produced by a subconscious change of the stroker's body language or attention toward the animal during live talking. However, stroker behavior was standardized as far as possible – in both conditions, the stroker was calmly sitting next to the heifer's shoulder, focused on stroking the animal. Great care was taken to match the "playback" condition not only in body posture and calm breathing, but also in mental focus and intention of interacting gently with the animal, trying to minimize possible differences in non-verbal communication.

We hypothesized that the higher degree of standardization in the "playback" stimulus would lead to decreased variability in the data. However, the variability of the responses as indicated by the precision parameters revealed a conflicting pattern, indicating that the relationship between the degree of standardization of the treatment and the variability in the observed behavior is more complex than expected or has different effects on different parameters. The higher degree of standardization in "playback" stimuli did not lead to a generally reduced variability and therefore should not be the main criterion for preference of playback stimuli for gentle human-animal interactions in experimental settings.

CONCLUSION

Our experiment leads to the conclusion that gentle stroking in combination with gentle vocal stimulation can induce positive affective states in habituated heifers, both when the experimenter is talking directly to the animal and when the vocal stimulus is played back from a recording. However, changes in cardiac parameters point toward a more positive experience and longer-lasting relaxation effects of live talking. Taking into account the inconclusive results regarding the effects of a higher degree of standardization on the variability of the data, we conclude that the use of recorded auditory stimuli to promote positive affective states in human-animal interactions in experimental settings is possible, but not necessarily preferable.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Ethics and Animal Welfare Committee of Vetmeduni Vienna (Ethik und Tierschutzkommission), project number ETK-02/04/2017; Veterinärplatz 1, 1210 Vienna.

AUTHOR CONTRIBUTIONS

SL and SW: conceptualization. SL, SW, LB, AL, and AF: methodology. AL: formal analysis, visualization, and writing—original draft preparation. AL and LB: investigation. SL, SW, and AL: writing—review and editing. SW: supervision. SL: project administration and funding acquisition. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.579346/full#supplementary-material

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Rapid Learning and Long-Term Memory for Dangerous Humans in Ravens (*Corvus corax*)

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Like many predatory species, humans have pronounced individual differences in their interactions with potential prey: some humans pose a lethal threat while others may provide valuable resources. Recognizing individual humans would thus allow prey species to maximize potential rewards while ensuring survival. Previous studies on corvids showed they can recognize and remember individual humans. For instance, wild American crows produced alarm calls toward specifically masked humans up to 2.7 years after those humans had caught and ringed them while wearing that mask. However, individual behavior of the crows or the impact of social features on their responses, was hardly examined. Here, we studied predator learning and social effects on responses, using a similar method, in captive common ravens (*Corvus corax*). We investigated learning and the impact of key social components on individual reactions to artificial predators. Human experimenters wore two types of masks while walking past two raven aviaries. In four training trials, the "dangerous" mask was presented while carrying a dead raven, whereas the "neutral" mask was presented empty-handed. Between every training trial and in all following trials, we presented both masks without dead ravens. We assessed the subjects' (i) learning speed, (ii) selective long-term response, and (iii) potential effects of social dynamics on individual alarm calling frequency. Ravens learned quickly (often based on the first trial), and some individuals distinguished the dangerous from the neutral mask for the next 4 years. Despite having received the same amount and quality of exposure to the dangerous mask, we found pronounced individual differences in alarm calling that were fairly consistent across test trials in socially stable situations: dominance, but not sex explained individual differences in alarm responses, indicating the potential use of alarm calls as "status symbols." These findings fit to those in wild bird populations and dominant individuals signaling their quality. Changes in the individuals' participation and intensity of alarm calling coincided with changes in group composition and pair formation, further supporting the role of social context on ravens' alarm calling.

Keywords: predator recognition, corvid, raven (*Corvus corax*), alarm call, memory, learning, individual human recognition

INTRODUCTION

Learning about new predators allows individuals to adapt existing anti-predator behavior to new threats. Many animal species are able to recognize conspecifics on an individual level (Tibbetts and Dale, 2007; Wiley, 2013), and several taxa have been shown to learn to recognize novel predators on a species level (Griffin et al., 2000). However, studies showing individual recognition of (potentially dangerous) members of other species remain rare. Anti-predator behavior is risky and reduces time and energy for other contexts like foraging and reproduction (Montgomerie and Weatherhead, 1988; see Lima and Dill, 1990 for a review). Limiting predator responses to specific individuals rather than generalizing to an entire species should therefore be adaptive (Berzins et al., 2010). For instance, individuals of the same predator species may differ substantially in their hunting abilities, because of sexual size dimorphism, different levels of experience with prey etc. (e.g., Hakkarainen et al., 1996). Indeed, studies on tits showed them capable of assessing the risk posed by individual predators, for example by adjusting referential warning calls and behavioral responses depending on the predator's size (Templeton et al., 2005; Courter and Ritchison, 2010). For human individuals, such differences in behavior may even be pronounced: what humans do in interaction with specific individuals of another species can vary substantially, ranging from providing food and shelter to hunting. Several species have adapted to humans' presence, i.e., urbanization, better than others (Shochat et al., 2006; Kark et al., 2007), and several species in close contact with humans have been shown to recognize human faces (Davis, 2002). Recent studies investigating individual predator recognition, predominantly in birds, therefore used humans as test stimuli (Cornell et al., 2012; Swift and Marzluff, 2015; Lee et al., 2019).

Most birds use mobbing as an anti-predator behavior. Mobbing is a coordinated action of multiple individuals of a weaker species against one or more individuals belonging to a more powerful species (Hartley, 1950). Mobbing behaviors can range from uniform, harsh predator directed alarm calls (scolding) to physical attacks (Altmann, 1956) and primarily serve to harass predators into leaving. Aside of moving off predators, mobbing may also function as signal of (male) quality and/or status (Slagsvold, 1984; Ellis, 2009; Tanager, 2011), and an opportunity for young to learn to recognize predator species (Curio, 1978; Curio et al., 1978a,b). Specifically, corvids have frequently been tested for individual predator learning: American crows (*Corvus brachyrhynchos*) have been shown to learn about novel predators and remember for at least 2.7 years (Marzluff et al., 2010). Experimenters wore masks while catching and ringing wild crows. The directly handled crows remember the masks worn during catching and responded with significantly higher scolding intensity than toward the control masks. Additionally, nearby observer crows who were not handled did so as well. A follow-up study provided experimental evidence of social transmission of predator-knowledge, as individuals not present during the catching event produced alarm calls when confronted with the "dangerous" mask (Cornell et al., 2012). In a second follow-up study, American crows were again exposed to masked humans, this time carrying a dead conspecific (Swift and Marzluff, 2015). The crows responded with alarm calls and avoidance of areas where the presentations occurred, and the response lasted at least 7 weeks. Similar studies on wild jackdaws (*Corvus monedula*) showed that these birds can learn to recognize individual humans by their facial features (Davidson et al., 2015). Experimenters approached jackdaws while wearing two types of masks, one of which was previously worn while handling their eggs; the "dangerous" mask later elicited longer latencies to return to the nest box than the neutral mask. In a further step, playbacks of conspecific alarm calls were coupled with the presentation of a masked human (Lee et al., 2019). In later presentations, without the playback, the birds showed increased latencies to return to their nest boxes when the masked human was nearby, but not when presented with a control mask.

Taken together, these studies provide experimental evidence of predator learning in corvids, specifically when using masked humans as novel predators. Training events like catching or presentation of dead conspecifics (for American crows), handling of the nests or playback of alarm calls (for jackdaws) were restricted to single events or periods lasting no more than 3 days. Yet in all cited studies, obvious differences in behavioral response to the different masks were documented, indicating quick learning capabilities. Because several of these studies have been conducted on wild populations, the control over individual exposure intensity was intrinsically limited (e.g., for crows), or the tests were restricted to short time periods only (e.g., for jackdaws). Hence, individual variation in birds' anti-predator responses have hardly been investigated for consistency over time and different social settings.

The current study focuses on another member of the corvid family, the common raven (*Corvus corax*). Outside the breeding period, ravens tend to form groups with moderate to high degrees of fission-fusion dynamics. Throughout the day, they split from large roosting-flocks of up to several 100 individuals and forage in sub-groups of varying composition (Braun and Bugnyar, 2012), in which individuals may meet each other repeatedly at one or more locations (Loretto et al., 2017). Depending on the food source and foraging strategies, these sub-groups may range from a few (2–5), to around 20 or up to 100 birds (Marzluff and Heinrich, 1991; Dall and Wright, 2009; Braun and Bugnyar, 2012). It has been hypothesized that these social conditions favor the emergence of sophisticated forms of cognition (Whiten and Byrne, 1988; Dunbar, 1998; but see DeCasien et al., 2017) including long-term memory for individuals (Fiore et al., 2008). Previous studies revealed that ravens possess long-term memory of the relationship valence to former group members (Boeckle and Bugnyar, 2012). Social context and group compositions also affect ravens' risk-taking behavior (Stöwe et al., 2006). Furthermore, a series of studies indicated that ravens can pay close attention to human facial features like gaze direction (Bugnyar et al., 2004; Schloegl et al., 2007), making them well-suited for the purpose of our study: long-term memory for heterospecific individuals (in this case, humans).

Similar to the work on crows and jackdaws (e.g., Swift and Marzluff, 2015; Lee et al., 2019), we had a human presenter wearing one of two types of masks: one mask was worn with the experimenter carrying an unfamiliar dead raven in one hand, simulating the outcome of a predation event; the other “neutral” mask was worn by an experimenter with both hands empty. Unlike the previous studies, we tested captive birds in their social groups, i.e., the presenter walked past the aviaries of a captive raven colony. We thus had full control over each individual’s exposure to the training stimulus, which allowed us to examine individual variation in the ravens’ responses within and across experimental presentations and to investigate the effects of individual and social features on alarm calling participation. Notably, we tested the ravens’ discrimination between the “dangerous” and neutral mask on a long-term basis, by presenting both masks without reinforcement (i.e., experimenter empty-handed) for 4 years. During this time, group compositions changed from two initial groups of eight individuals each, to one large group of 12, and finally to multiple pairs. In the first 3 years, we also recorded focal protocols analyzing daily life situations, from which we extracted information about dominance relationships.

We predicted that the ravens would quickly learn to discriminate between masks, leading to higher scolding intensities (i.e., longer duration of alarm calling) for the dangerous mask than for the neutral mask. Based on previous reports and own pilot observations, we also predicted substantial individual variation in alarm calling intensity, potentially explained by individual-specific features like sex, raising type, and kinship, and/or by social features like group composition and dominance. Based on previous findings in corvids, we hypothesized that ravens would continue discriminating between the masks over a long time period, possibly years, without reinforcement (i.e., without the pairing with a dead raven). Furthermore, we expected that individual variation in scolding would be consistent across experimental presentations, as long as the group composition remained stable.

TABLE 1 | List of individuals. For ease of identification, single-individual sib-groups were named after individuals.

Name	Initial group	Sex	Year hatched	Raising	Sib-group
Anton	A	Male	2010	Parent-raised	3
Ellen	A	Female	2010	Parent-raised	4
Heidi	A	Female	2010	Parent-raised	3
Jakob	A	Male	2010	Parent-raised	4
Jonas	A	Male	2010	Parent-raised	2
Klara	A	Female	2010	Parent-raised	4
Lena	A	Female	2010	Parent-raised	1
Sophie	A	Female	2010	Parent-raised	1
Astrid	B	Female	2010	Hand-raised	2
Joey	B	Female	2010	Hand-raised	Joey
Lellan	B	Female	2011	Hand-raised	Lellan
Matte	B	Male	2011	Hand-raised	Matte
Orm	B	Male	2011	Hand-raised	Orm
Ray	B	Male	2011	Hand-raised	Ray
Skadi	B	Female	2011	Parent-raised	5
Thor	B	Male	2011	Parent-raised	5

MATERIALS AND METHODS

Ethical Note

This experiment was approved by the animal ethics and experimentation board of the University of Vienna under the license number 2018-011. The entire data collection was non-invasive.

Subjects and Housing

Study subjects were 16 captive ravens (**Table 1**) housed in two large aviaries at the Haidlhof Research Station, an outdoor facility of the University of Vienna and the University of Veterinary Medicine, Vienna, located near Bad Vöslau, Lower Austria. At the begin of the study in 2011, birds were kept in two social groups of eight subjects each: Group A consisted of five females and three males; they were the offspring of four captive breeding pairs, were raised from hatching to fledging by their parents in 2010 and arrived at Haidlhof in September of that year. Group B consisted of four females and four males; they originated from captive and wild breeding pairs (three and five birds, respectively) and were raised to fledging by their parents (two) or human foster parents (six in total). Two hand-raised females hatched in 2010, all others hatched in 2011 and arrived at Haidlhof in September of that year. Over the years, all ravens were exposed to changes in group composition and size, simulating the dynamics under natural conditions (compare Braun and Bugnyar, 2012) and adhering to the birds’ maturation and their transition from non-breeding to breeding state (compare Heinrich, 1999). In October 2012, four birds of Group A left the station, and the remaining individuals were merged into one group. Over the following 2 years, the non-breeder group consistently became smaller as individuals pair-bonded and were transferred into separate compartments for breeding. Pairs continued to be included in the experiment as long as they were kept at Haidlhof. Five individuals left the station in 2014 and three more in 2015; 2015 represents the end of this study as only two birds remained at Haidlhof the following years.

All birds were marked with colored rings for individual identification. Each aviary had smaller chambers attached that provided opportunity for shelter and visually isolated retreating opportunities, but remained closed during experiments. Multiple branches provided enrichment and perching opportunities. The ground substrate consisted of gravel, wood chips, and sand. The birds were fed twice a day with a diet of meat, grain products, fruits, and vegetables and had access to water *ad libitum*.

Experimental Procedure

The experiment lasted from October 2011 to October 2015 and consisted of three phases. In the initial control phase (October 2011), human presenters wore standardized clothing (gray poncho, rubber boots, and gloves) and one of two masks (**Figure 1**). The hood of the poncho was worn over the back of the head and the top of the mask to keep the natural hair of the presenters out of view. Wearing one mask, the presenter approached the first aviary and remained still for 2 min. They then moved to the opposite end of the aviary and stood still for another 2 min to ensure that all individuals would have an opportunity to see the mask (**Figure 2**). The presenter then continued to the second aviary and repeated the procedure. The total duration of the presentation was approximately 10 min. After a break of 30 min, the procedure was repeated with the other mask. Data collection started with a 10-min baseline before each presentation, to ensure no additional events would occur that elicit an alarm response (e.g., birds of prey above the aviary). In such cases, the presentations were postponed. Trials consisted of two presentations per day (one per mask) in the early afternoon and occurred twice a week. Masks were always worn by an actual human, dressed as described above, and the ravens never saw a separate mask alone. Please note that both aviaries were so close together that as soon as the experiment started, the presenter was in view for all individuals. This is also why we did not counterbalance the mask types. Due to the spatial arrangements of the aviaries, the presenter spent the first 4 min in front of the first group (but seen also by the second group), and the next 4 min in front of the second group (but seen also by the first group). However, all individuals had the same exposure time, i.e., 2 × 2 min close-up and 2 × 2 min further away.

FIGURE 1 | Mask presenter in standardized clothing holding a dead raven. Clothing consists of black rubber boots, white rubber gloves, and an olive plastic poncho. On the right are the black-haired dangerous mask and the red-haired neutral mask.

In the following training phase (October 2011–November 2011), the black-haired (hereafter "dangerous") mask was presented together with a dead raven. The dead raven was collected at our field site in the Alps close to the Konrad Lorenz Research Station; it was an adult wild bird killed by captive wolves at the Cumberland Wildpark and thus unfamiliar to our captive ravens at Haidlhof Research Station. The dead raven was shaken; its wings spread and then dropped and picked up at each location. This was an opportunity for the ravens to associate a potential outcome of predation with the "dangerous" mask. There were four trials where a dead conspecific was presented with the dangerous mask. In contrast, the presentation of the neutral mask was performed empty-handed, i.e., neither a dead raven nor any other object was carried by the person when dressed up with this mask. Between every training trial, there was one additional trial where both masks were presented without the dead raven to test for learning speed. Two trials occurred per week.

In the final test phase (November 2011–October 2015), the precision and persistence of these associations were tested by further presentations of both masks without the dead raven. Trials occurred twice per month until May 2012, once a month until November 2013, three times in 2014, and once in 2015.

Across the entire data collection period, both presentations per trial were carried out on the same day and by the same person. We used 17 different presenters for a total of 39 trials. We documented individual scolding durations using video recordings (Canon Legria HF S10, Canon Legria HF S30). Video analysis was performed on PC with the use of Solomon Coder (Péter, 2011).

Statistics

Analysis was conducted in R (version 3.6.1; R Core Team, 2019) using general linear mixed models (GLMMs) with a beta distribution (using the function "glmmTMB" in the package "*glmmTMB*"; Brooks et al., 2017) and logit link.

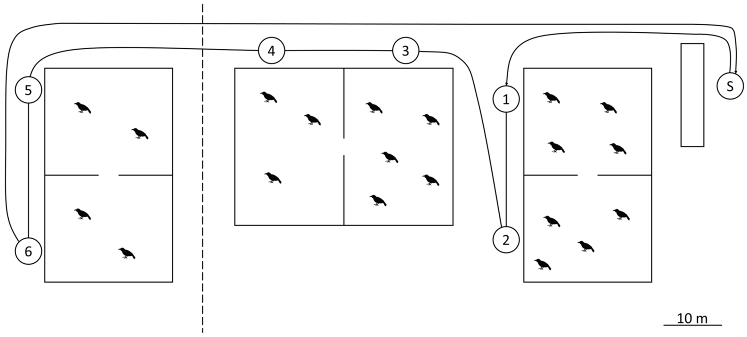

FIGURE 2 | Plan of the aviaries. A barn on the far right provides visual cover for the start of the presentation, marked with "S." Numbered circles show the presentation locations per aviary. The leftmost aviary was only used after the training phase, when groups got split into pairs. Presentations were only carried out in front of occupied compartments.

Theoretically identifiable random slopes and dispersion parameters were assessed using functions provided by Roger Mundry. Variance inflation factors (VIFs) were determined using the function "vif" of the package "*car*" (version 3.0.8; Weisberg and Fox, 2011).

Model 1: Learning

During our data collection, the size and number of our groups changed and some additional compartments were included while others were empty and skipped. This resulted in different durations where the mask was in view of the subjects (mean = 223.0 s, *SD* = 88.3 s). We therefore calculated the alarm calling response as proportion of the presentation duration. We linearly scaled our response to a range between 0 and 1 and used a beta distribution. This allowed us to include differences in response intensity which would have been lost in a binomial model.

Prior to analysis, we *z*-transformed all covariates to a mean of 0 and a standard deviation of 1 to increase interpretability and facilitate convergence (Schielzeth, 2010). To provide comparability with other datasets, we list the means and standard deviations for time since training (in days, mean = 356.4, *SD* = 341.3) and group size (mean = 7.3, *SD* = 2.7). We calculated sex ratios for all groups ranging from 0 (all female) to 1 (all male). Finally, we centered and dummy coded all factors with the reference levels being neutral for mask, first for order, female for sex, one for sib-group, and hand-raised for raising. Sib-group only indicates family relation, not necessarily that the siblings were housed or raised together (**Table 1**).

As response, we used proportion of time spent alarm calling (as described above). As test predictors, we included mask type (dangerous or neutral), sex (male or female), raising type (hand- or parent-raised), and kinship of subject (families indicated by numbers, individuals without siblings by names), and size and sex ratio of the group as fixed effects. As control predictors, we included further fixed effects for order of presentation (first or second presentation of the day), age of the subjects, and days since the last training presentation. As random intercept effects, we included individual and presenter. To reduce type 1 errors, we included theoretically identifiable random slopes (Schielzeth and Forstmeier, 2009; Barr et al., 2013), specifically of age, time since training, mask type, order of presentation, group size and sex ratio within individual and of age, mask type, order of presentation, raising, sex, group size, sex ratio, and sibling-group within presenter. Sample size was 722 observations of 16 individuals. This maximal model did not converge, so we used a reduced model by dropping random slopes of sibling-groups from presenter.

We used the function overdisp.test (provided by Roger Mundry) which returned a dispersion parameter of 0.72 and therefore smaller than 1, confirming that the model is not overdispersed. Slight underdispersion potentially leads to conservative test results and is not generally considered problematic. Collinearity of test predictors was determined for a standard linear model lacking the random effects and appeared to be no issue (maximum VIF: 3.1; Quinn and Keough, 2002).

We conducted a full-null model comparison (Forstmeier and Schielzeth, 2011) to check the overall effect of our test predictors and to avoid cryptic multiple testing. The null model lacked the test predictors but was otherwise identical to the full model (including the same fixed effects for control predictors as well as the same random intercept effects and random slopes). The comparison was based on a likelihood ratio test (function "ANOVA" with "test" argument set to "Chisq"; Dobson, 2002). To investigate differences between sibling-groups, we ran a *post hoc* test by changing the reference levels of "sib-group" (with the command "relevel") and running separate models for every respective level of sib-group.

Model 2: Dominance

To investigate potential influences of dominance on alarm calling behavior, we used a second model including calculated Elo ratings based on won vs. lost conflicts (Albers and de Vries, 2001). This method assigns a new individual rating after every conflict, based on the outcome and the participants' previous rating. A win against a high-ranking individual is therefore worth more points vs. a low-ranking individual, as is a won high-intensity conflict (e.g., fight) vs. a won low-intensity conflict (e.g., threat). We used data gathered from ongoing, station-wide social focal protocols (5-min individual focal sampling; Altmann, 1974, three times per week) and conducted the analysis in R (using the function "elo.seq" in the package "EloRatings"; Neumann and Kulik, 2020). We set a manual k-factor (i.e., point value) for specific conflict behaviors (fight = 200, chase = 100, challenge = 60, displacement = 40, and threat = 20) and calculated Elo ratings for each individual per group composition which were then scaled to a range of 0–1. Pairs were excluded and video protocols were unavailable for some group compositions and years, resulting in available data for 5 out of 16 group compositions and covering the first 3 years of data collection, reducing our sample size from 722 to 338 observations.

The model formula is similar to model 1, with the addition of a fixed effect for Elo ratings as the only test predictor. As random intercept effects, we again included individual and presenter. We included random slopes of Elo ratings in both individual and presenter but could no longer identify them for age and group size in presenter, so we removed them (this is explained by the reduced sample size covering a smaller number of presentations). Both the dispersion parameter (0.68) and the maximal VIF (3.7) were within acceptable limits. We conducted a full-null model comparison following the same procedure as for model 1 with the null model lacking a fixed effect for Elo ratings, but being otherwise identical to the full model.

Model 3: Persistence

Both previous models investigate effects on the overall scolding participation per predictor. To test if the distinction between the masks changed over time, i.e., persistence, we ran a third model using as response the proportion of scolding the bad mask minus proportion of scolding the neutral mask.

We again linearly scaled the response between 0 and 1 and fitted a third beta model using the same approach as described above. As test predictors, we included time since training, sex, raising and kinship of the subject, and size and sex ratio of the group as fixed effects. As random intercept effects, we included individual and presenter with random slopes of time since training in individual, raising and sex in presenter, and group size and sex ratio in both. Sibling-group was originally included in presenter but was dropped due to convergence issues. Sample size spanned 361 observations.

There were no issues with overdispersion (dispersion parameter 0.80) or collinearity (maximum VIF 3.1). The null model used for model comparison included only the random intercept effects with the random slopes, but no fixed effects.

RESULTS

All but one raven (male Ray) participated in active scolding of a human wearing a mask in the test phase, even though neither mask was paired with a dead raven at that time any longer. However, individuals varied strongly in their overall scolding participation (whether or not they engaged in scolding; **Figure 3**) and in their scolding intensity per mask (how long they engaged in scolding; **Figure 4**). In each of the two original groups, a particular sibling pair (Anton and Heidi in Group A; Thor and Skadi in Group B) took the lead in scolding in respect to both participation and intensity; the males of these pairs were the dominant males in their groups. After the removal of the dominant male of Group A (Anton) and the fusion of the two groups, Jonas became the dominant male and also increased his scolding participation and intensity.

When plotting group averages of scolding response per mask type across time, visual inspection of the graph indicates learning and memory effects (**Figures 5, 6**). We tested for these effects in addition to effects of individual and social factors (like sex, raising style, kinship, group size, and sex ratio) *via* three statistical models.

Model 1: Learning

Overall, our test predictors (mask type, sex, raising and kinship of subject and size and sex ratio of the group) had a significant impact on scolding response (full-null model comparison: $\chi^2 = 49.506$, $df = 14$, $p < 0.001$). As expected, subjects spent more time producing alarm calls toward the dangerous mask than toward the neutral mask in the test phase (**Table 2**). Additionally, social context contributed to individual variation: larger group-sizes correlated with shorter times spent scolding per individual and higher ratios of males in the group with increased scolding duration (**Figure 6**). Furthermore, individuals that were raised by ravens showed longer alarm responses than those raised by humans (**Figure 6**). We found no significant effects for sex. Finally, there were differences in scolding duration between sibling-groups (**Figure 7**). *Post hoc* testing revealed significant differences for group 4 when compared to groups 1, 2, 5 and Joey ($p < 0.001$ in all cases) and a trend for the comparison of groups 5 and 2 ($p = 0.054$).

Model 2: Dominance

The full-null model comparison, with Elo ratings being the only test-predictor, was significant ($\chi^2 = 8.398$, $df = 3$, $p = 0.038$). Focusing on the 3-year time period for which information on dominance relationships was available, we found that individuals with higher Elo ratings showed longer scolding durations (**Table 3, Figure 8**).

Model 3: Persistence

Other than models 1 and 2, we now used as response the difference in scolding duration between the masks (dangerous minus neutral), rather than scolding duration in general. The combination of test predictors (time since training, sex, raising

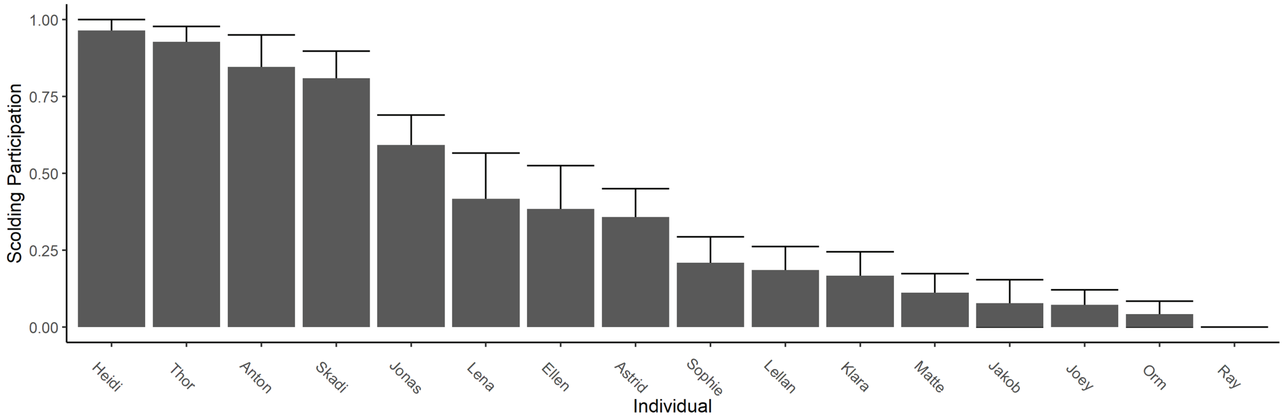

FIGURE 3 | Scolding participation in test phase. Bars show participation in scolding as the proportion of presentations in which the individual produced at least one alarm call. Whiskers show SEs. Across the entire test phase, one individual never participated (male Ray).

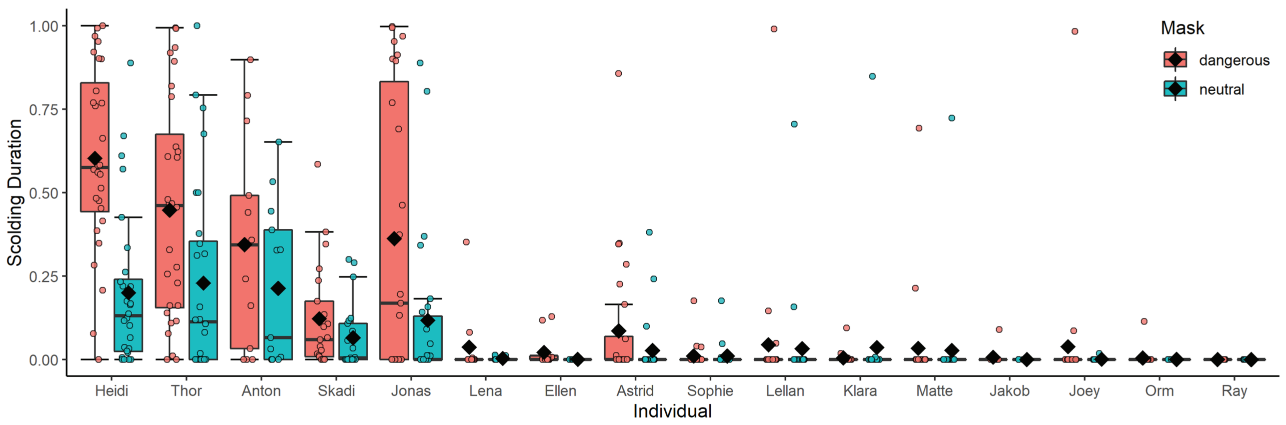

FIGURE 4 | Scolding intensity in the test phase per mask. Individuals are ordered by participation. Black diamonds show means. Only one individual (female Klara) scolded the neutral mask more than the dangerous mask.

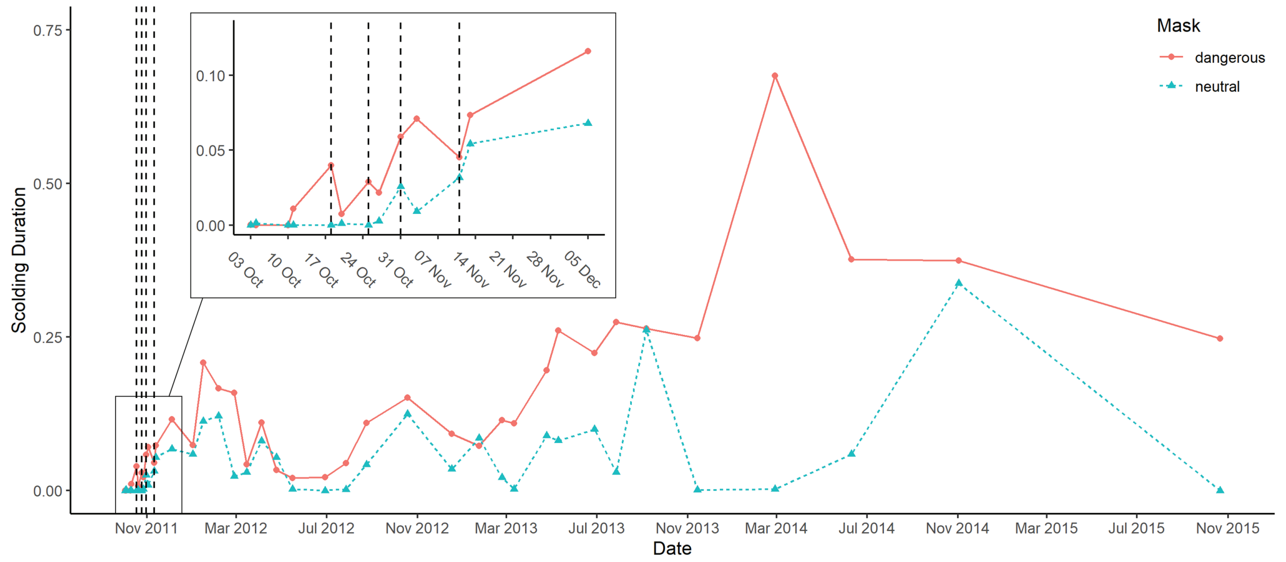

FIGURE 5 | Group averages of scolding response per mask across all phases. The control phase consisted of four trials over 2 weeks, the training phase of four trials with and three trials without dead raven in alternating order over 4 weeks (trials where the dangerous mask was presented while carrying a dead raven are marked with vertical lines) and the test phase consisted of 28 trials over 4 years.

and kinship of the subject and size and sex ratio of the group) had a significant effect on mask-distinction (full-null model comparison: $\chi^2 = 29.096$, $df = 14$, $p = 0.010$). Notably, we found no changes in distinction between the masks across time in the test period (**Table 4**, **Figure 5**). Parent-raised individuals responded to the dangerous mask stronger than hand-raised individuals (**Figure 6**). The model also revealed that some sibling-groups discriminated better than others (**Figure 7**), and overall the discrimination was better when more males were present (**Figure 6**). We found no significant effects of caller sex or group size.

DISCUSSION

Captive ravens quickly learned to distinguish human experimenters wearing one of two masks, whereby the "dangerous" mask was initially paired with the presentation of a dead conspecific and the neutral mask was not. In subsequent tests without a dead raven, ravens scolded more toward humans wearing the dangerous mask than the neutral mask; furthermore, they continued to do so over a 4-year period without further experimental reinforcement. Despite having received the same amount and quality of exposure, individual birds differed strongly in how

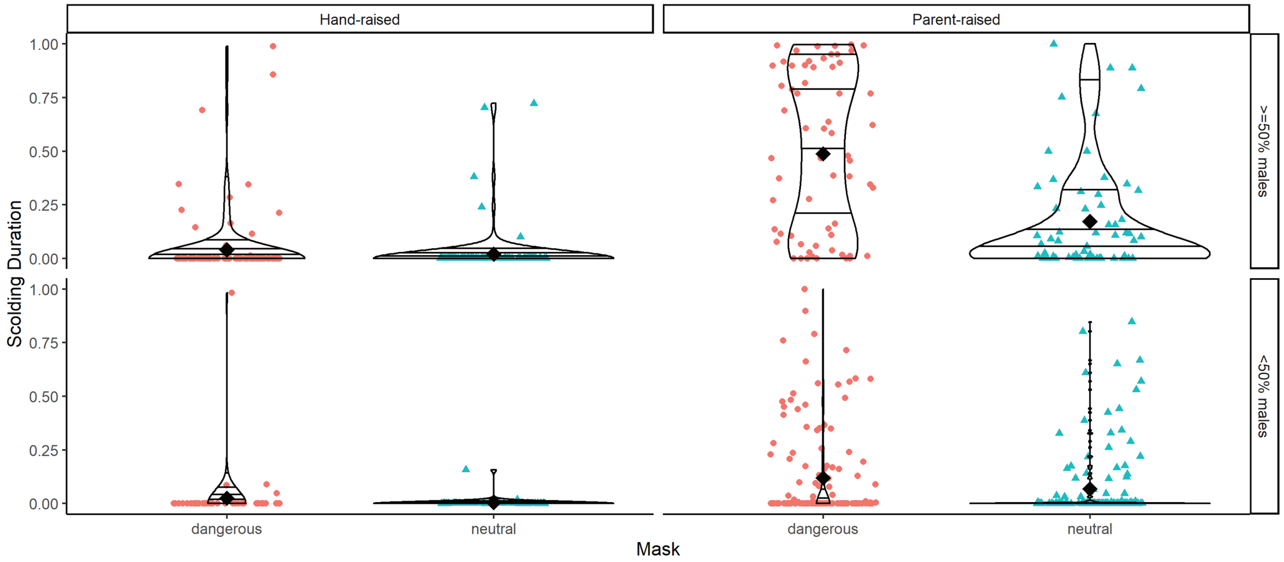

FIGURE 6 | Violin plots of scolding duration as proportion per mask type (dangerous vs. neutral), raising type (hand-raised vs. parent-raised), and group sex ratio (more females than males vs. equal or more males than females). Horizontal lines within the violin plots show quantiles set at 0.25, 0.5, 0.75, and 0.95. Black diamonds show means.

TABLE 2 | Output from Model 1 on long-term memory.

Fixed effects	Estimate	*SE*	*z* value	*p* value	
(Intercept)	−4.67	0.98	−4.76	<0.001	***
Dangerous mask	0.43	0.18	2.40	0.017	*
Order 2nd	−0.26	0.17	−1.53	0.126	
Sex male	−0.08	0.16	−0.48	0.631	
Age	1.82	1.73	1.05	0.293	
Sib-group 2	0.41	0.27	1.54	0.123	
Sib-group 3	1.72	0.21	8.17	<0.001	***
Sib-group 4	−0.04	0.18	−0.20	0.843	
Sib-group 5	2.86	1.93	1.48	0.139	
Sib-group Joey	0.38	0.35	1.08	0.282	
Sib-group Lellan	2.50	1.93	1.29	0.197	
Sib-group Matte	2.54	1.95	1.30	0.193	
Sib-group Orm	2.53	1.95	1.30	0.195	
Sib-group ray	2.47	1.95	1.27	0.205	
Raising parent	0.78	0.29	2.68	0.007	**
Sex ratio	3.24	0.73	4.44	<0.001	***
Group-size	−0.11	0.04	−2.66	0.008	**
Time since training	−1.66	1.48	−1.13	0.260	

*General linear mixed model (GLMM) output showing fixed effects with response as proportion of scolding. Age and time since training were z-transformed, the rest dummy coded with the reference categories being neutral (for mask), first presentation (for order), 1 (for sib-group), and hand-raised (for raising). Higher sex ratios indicate more males. N = 722. Significance codes: <0.1; * < 0.05; ** < 0.01; *** < 0.001.*

often and/or how long they participated in scolding the masked humans. This inter-individual variation was largely explained by social factors and fairly consistent across experimental presentations in socially stable situations. Later changes in the individuals' scolding participation and/or intensity coincided with changes in group composition and pair formation.

Learning

Ravens quickly learned to distinguish between humans based on their facial features, which is in line with the results of previous studies on other corvids (Levey et al., 2009; Marzluff et al., 2010; Lee et al., 2011; Davidson et al., 2015). As in American crows (Swift and Marzluff, 2015), seeing a dead conspecific being carried by a human was enough to form an association between this putative predation event and the facial features of that person, i.e., his or her mask. Note that we used different human presenters across the experiment, but always had the same person present both masks during each test round; this procedure makes it unlikely that the ravens based their discrimination on any other human features (body shape, movement, odor, etc.) but the masks. During our control phase before training, we observed hardly any scolding response to either mask. Thus, we can rule out that the ravens had a general aversion to masked humans or an initial preference or dislike for one mask over the other. Hence, we argue that the ravens assigned different threat levels to the two masks as a result of the four training trials with a dead conspecific. However, as our neutral mask was always presented empty-handed, the possibility remains that the ravens' assignment of different threat levels might be generally caused by a human carrying an item (and not a dead raven).

Dominance and Social Features

A noteworthy result of our study was the high individual variation in scolding participation, despite the equal and highly controlled exposure experienced by all birds. This variation could be explained by a mix of factors: Model 1 revealed effects of kinship, i.e., sibling groups participating either strongly

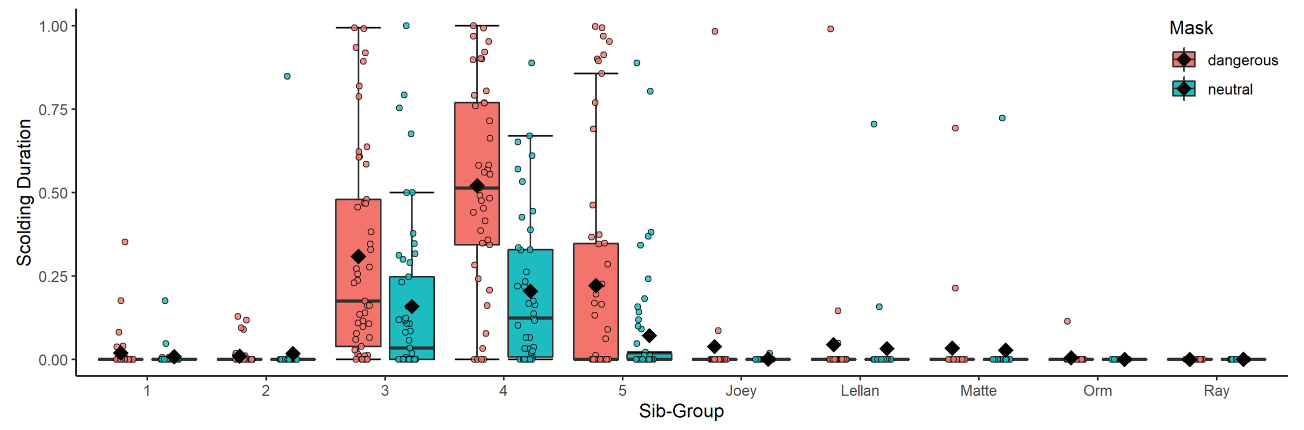

FIGURE 7 | Boxplots of scolding duration as proportion per mask and sib-group. Black diamonds show means. Sib groups indicate only kinship and individuals of the same family were not necessarily housed in the same aviary-compartment or raised together.

TABLE 3 | Output from Model 2 on dominance.

Fixed effects	Estimate	*SE*	*z* value	*p* value	
(Intercept)	−9.74	6.57	−1.48	0.138	
Mask dangerous	0.28	0.12	2.29	0.022	*
Order 2	−0.15	0.10	−1.42	0.156	
Sex male	−1.56	0.41	−3.85	<0.001	***
Age	−3.04	1.80	−1.68	0.092	
Sib-group 2	0.16	0.33	0.47	0.635	
Sib-group 3	1.56	0.29	5.37	<0.001	***
Sib-group 4	−0.26	0.22	−1.18	0.240	
Sib-group 5	−3.86	3.41	−1.13	0.257	
Sib-group Joey	0.95	0.51	1.87	0.061	
Sib-group Lellan	−4.49	3.33	−1.35	0.178	
Sib-group Matte	−3.57	3.37	−1.06	0.289	
Sib-group Orm	−4.07	3.36	−1.21	0.226	
Sib-group ray	−3.78	3.36	−1.12	0.261	
Parent-raised	1.42	0.99	1.44	0.150	
Sex ratio	−1.63	7.17	−0.23	0.820	
Group-size	0.92	0.50	1.86	0.063	
Time since training	0.98	0.91	1.08	0.279	
Dominance	2.41	0.51	4.75	<0.001	***

*GLMM output showing fixed effects with response as proportion of scolding. Elo ratings for dominance were scaled from 0 to 1, age and time since training were z-transformed, the rest dummy coded with the reference categories being neutral (for mask), first presentation (for order), 1 (for sib-group), and hand-raised (for raising). Higher sex ratios indicate more males. N = 338. Significance codes: < 0.1; * < 0.05; ** < 0.01; *** < 0.001.*

or weakly in scolding (**Figure 7**). It remains unclear what the basis for these sibling effects might be, e.g., genetics, epigenetics, or social constraints (Champagne, 2008; Oliveira, 2009; Taborsky et al., 2012). We also found a negative effect of group size, indicating a potential dilution effect (Hamilton, 1971; Foster and Treherne, 1981; Lima and Dill, 1990).

Unlike Buitron (1983) we found no effects of caller sex, but we saw higher scolding durations in groups with higher ratios of males, possibly indicating male competition using scolding as status signal. This interpretation is further supported by dominant individuals producing more alarm calls (status signals), and the fact that in ravens males are typically more dominant than females (Harriman and Berger, 1990; Stöwe et al., 2006). Model 2 showed dominance to be one of the strongest predictors for scolding intensity overall. Previous studies on captive jungle fowl (*Gallus gallus*) confirmed higher mating chances for males that produce more alarm calls (Wilson et al., 2008), and showed positive correlations of anti-predator behavior and dominance (Pizzari, 2003). Studies on another corvid, the Siberian Jay, showed increased mobbing intensity for breeding alpha males within kin-groups, specifically in presence of their own offspring (Griesser and Ekman, 2005). A follow-up study argues that mobbing events of adult conspecifics would provide opportunity for predator-learning to the offspring (Griesser and Suzuki, 2017). We found a similar increase in scolding in paired adults, but in the absence of any offspring. We thus interpret the intensive scolding by dominant ravens to have other functions than predator-learning in offspring, like signaling status and/or quality (Slagsvold, 1984; Ellis, 2009; Tanager, 2011). The latter is supported by a study showing that males across 19 species increase their mobbing intensity in the presence of females (da Cunha et al., 2017a), and a comparison of 145 species of birds concluding that different social systems do not influence mobbing behavior (da Cunha et al., 2017b).

We also observed high-ranking individuals to aggressively challenge low-ranking individuals for producing intense scolding bouts (personal observation). However, because individuals tended to be close to the presenter while scolding, an alternative explanation would simply be redirected aggression toward the nearest subordinate group member (instances of re-direction have been observed in captive and free-ranging ravens, but not systematically studied). These dilution or suppressor effects could be responsible for the low scolding responses and failure to distinguish between the masks in some individuals, rather than a failure in learning to identify the masked human as potential threat. Disentangling these effects is not possible in our paradigm, but would be an interesting line of investigation

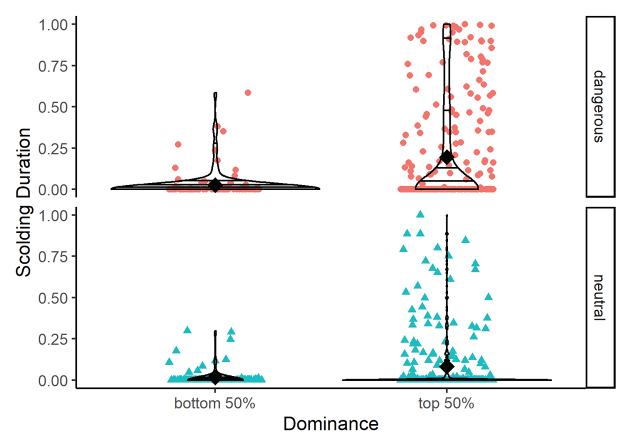

FIGURE 8 | Violin plots showing scolding duration as proportion per mask type (dangerous vs. neutral) and dominance (top 50% of dominant individuals vs. bottom 50%). Horizontal lines within the violin plots show quantiles set at 0.25, 0.5, 0.75, and 0.95. Black diamonds show means.

TABLE 4 | Output from Model 3 on memory.

Fixed effects	Estimate	SE	*z* value	*p* value	
(Intercept)	−0.85	0.37	−2.29	0.022	*
Sex male	0.06	0.12	0.51	0.609	
Sib-group 2	0.40	0.15	2.59	0.010	**
Sib-group 3	0.63	0.12	5.43	<0.001	***
Sib-group 4	−0.07	0.11	−0.64	0.522	
Sib-group 5	0.08	0.12	0.65	0.515	
Sib-group Joey	0.50	0.19	2.61	0.009	**
Sib-group Lellan	0.46	0.19	2.39	0.017	*
Sib-group Matte	0.36	0.25	1.42	0.156	
Sib-group Orm	0.40	0.26	1.57	0.115	
Sib-group ray	0.39	0.26	1.53	0.125	
Raising parent	0.57	0.16	3.52	<0.001	***
Sex ratio	1.35	0.44	3.04	0.002	**
Group-size	−0.03	0.03	−0.87	0.387	
Time since training	0.09	0.07	1.29	0.197	

*GLMM output showing fixed effects with response as difference in proportion of scolding per mask (dangerous – neutral). Age and time since training were z-transformed, the rest dummy coded with the reference categories being neutral (for mask), first presentation (for order), 1 (for sib-group), and hand-raised (for raising). Higher sex ratios indicate more males. N = 361. Significance codes: < 0.1; * < 0.05; ** < 0.01; *** < 0.001.*

for a follow-up study testing participating individuals in separation. If individuals distinguish between the masks in isolation, it would rule out a failure to learn, and support the presence of dilution or suppressor effects while in the group. By testing focus individuals in dyads with higher vs. lower ranking individuals, one could investigate dominance effects in more detail.

Finally, Model 1 also revealed an effect of rearing style, with parent-raised birds scolding the human presenters more readily and intensively. This is in accordance with the substantial literature on early life experiences, often showing long-term effects (Hemetsberger et al., 2010; Boucherie et al., 2020).

The upbringing by human foster parents likely made them less receptive for treating humans as potential predators. However, when hand-raised ravens engaged in scolding, they performed similarly to parent-raised birds and discriminated accurately between masks.

Patterns Across Time

Scolding intensity (to either of the masks) was rather low during training, and at the beginning of testing, but increased throughout the testing phase (**Figure 5**). A similar pattern has been observed in other avian species like mockingbirds (Levey et al., 2009), crows (Marzluff et al., 2010), magpies (Lee et al., 2011), and jackdaws (Davidson et al., 2015). One way to explain this pattern is that the presenters' disappearance after being scolded acts as reinforcement for future scolding (Knight and Temple, 1986; Griffin, 2004; Marzluff et al., 2010). The increased number of visits by masked persons could also elevate the perceived threat level, as reported for magpies (Redondo and Carranza, 1989; Lee et al., 2011). Conversely, one might argue that the repeated appearance of the dangerous person without any consequences reduces the perceived threat level, resulting in less fearful birds being more liberal in their scolding response (Marzluff et al., 2010). It is not possible to test these hypotheses with our current dataset, but additional presentations of the dangerous mask while carrying a dead conspecific, could again elevate a potentially lowered threat level. If afterward the scolding intensity did not decrease again, we could rule out that the birds were no longer perceiving the dangerous mask as a serious threat.

The discrimination between masks was hardly affected by the time elapsed since training in the experiment, suggesting that (at least some) ravens remembered the putative predation events for 4 years. While the dangerous mask elicited longer scolding durations throughout the study, we did notice some generalization, and thus increased calling, toward the neutral mask toward the end of the study period. This has also been observed in related studies on other corvids (Marzluff et al., 2010; Davidson et al., 2015), and in our case could be explained by the similarities between the two test conditions like identical clothing of the human presenters and the shared traits of the masks (e.g., their stiffness and glossiness). Given the low costs of scolding a masked person, and potentially high rewards of avoiding future predations (Marzluff et al., 2010), it is quite noteworthy that the ravens' responses to the neutral mask remained distinguishable from those to the dangerous mask for the entire study period.

While in all social constellations the dominant males of the groups took the lead in scolding, the majority of group members participated at low levels. The dominant males were accompanied in scolding by their siblings before they reached maturity (first 1–2 years of the study) and, after pair formation, by their female partners. Pair formation seemed to boost participation in scolding of (previously) subordinate females and males alike, which fits the finding that pair formation accompanies a rise in dominance status (Braun and Bugnyar, 2012). Taken together, these individual-level patterns support the notion that the social context is central to understanding ravens' participation in anti-predator behavior. While ravens seem to be fairly plastic in how much they contribute to scolding, their degree of consistency over time seems to be tied to social opportunities and constraints (see Lima and Dill, 1990 for a review; in birds: Hogstad, 1988; in mammals: Atwood and Gese, 2008; in fish: Brown et al., 2009).

Concluding Summary

Literature on heterospecific individual recognition is relatively rare, with the exception of recognition of human faces, which has been shown in variety of species, ranging from mammals, birds, and reptiles to invertebrates like octopuses and honeybees (Taylor and Davis, 1998; Davis, 2002; Dyer et al., 2005). However, testing methodology varied in most of these studies, which led to difficulty in comparing their results and conclusions (Dittrich et al., 2010). With the current study, we add to the recent literature investigating predator learning by using (masked) humans, reflecting a relatively standardized method of testing (Levey et al., 2009; Marzluff et al., 2010; Lee et al., 2011; Davidson et al., 2015). Similar to previous findings, we observed rapid learning after only four training presentations, resulting in behavior that reliably distinguished between the masks over 4 years. Because we worked with captive individuals, we obtained valuable additional information concerning large individual variation in scolding participation, intensity, and to some extent, level of discrimination between masks. This variation is mainly explained by social factors, notably dominance, and relative number of males in the group.

Although ravens regularly exploit human resources (Webb et al., 2004; Loretto et al., 2016), they typically do not live in densely human populated urban areas. The latter has been discussed as a key variable in explaining the ability of animals to discriminate between humans on an individual basis (e.g., Davis, 2002). We may thus wonder why ravens could (easily) come to recognize individual humans in the current study? On one hand, not only the frequency of exposure to humans may matter, but also the variation in human behavior toward the species in question. As scavenger, ravens have been exposed to humans as both "food providers" (that deliver garbage, animal kills etc.) and "predators" (that shoo them away or even hunt them) within their individual lives and for many generations (hundreds or thousands of years, Marzluff and Angell, 2005). They may thus have developed a predisposition to pay attention to individual features of humans that go together with their behavior. Selection for paying attention to human facial features has also been shown in domestic animals like dogs (Huber et al., 2013). On the other hand, discriminating between heterospecifics may come as a by-product of conspecific recognition, which has been proposed to be adaptive in social species (Tibbetts and Dale, 2007). Ravens may simply extend this ability to heterospecific individuals, which come to interact with them in relevant ways, i.e., as providers or predators. The latter interpretation would fit to several other species, for which differentiation among human individuals has been reported (Davis, 2002). Our study implies that social context shapes the expression of birds' knowledge about humans (or potential predators in general). Further investigation of the factors explaining the consistency and plasticity of inter-individual variation in corvids' behavior toward humans provides a promising line of future research.

DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by Animal Ethics and Experimentation Board Faculty of Life Sciences University of Vienna.

AUTHOR CONTRIBUTIONS

TB and CB designed the study. CB collected and analyzed the data and drafted the manuscript under the supervision of the other authors. TB and WF provided critical revisions to the manuscript. All authors approved the final version of the manuscript for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.581794/full#supplementary-material

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The Role of Animal Cognition in Human-Wildlife Interactions

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Humans have a profound effect on the planet's ecosystems, and unprecedented rates of human population growth and urbanization have brought wild animals into increasing contact with people. For many species, appropriate responses toward humans are likely to be critical to survival and reproductive success. Although numerous studies have investigated the impacts of human activity on biodiversity and species distributions, relatively few have examined the effects of humans on the behavioral responses of animals during human-wildlife encounters, and the cognitive processes underpinning those responses. Furthermore, while humans often present a significant threat to animals, the presence or behavior of people may be also associated with benefits, such as food rewards. In scenarios where humans vary in their behavior, wild animals would be expected to benefit from the ability to discriminate between dangerous, neutral and rewarding people. Additionally, individual differences in cognitive and behavioral phenotypes and past experiences with humans may affect animals' ability to exploit human-dominated environments and respond appropriately to human cues. In this review, we examine the cues that wild animals use to modulate their behavioral responses toward humans, such as human facial features and gaze direction. We discuss when wild animals are expected to attend to certain cues, how information is used, and the cognitive mechanisms involved. We consider how the cognitive abilities of wild animals are likely to be under selection by humans and therefore influence population and community composition. We conclude by highlighting the need for long-term studies on free-living, wild animals to fully understand the causes and ecological consequences of variation in responses to human cues. The effects of humans on wildlife behavior are likely to be substantial, and a detailed understanding of these effects is key to implementing effective conservation strategies and managing human-wildlife conflict.

Keywords: animal cognition, human-wildlife interactions, gaze sensitivity, individual recognition, class-level recognition, categorization, generalization, behavioral flexibility

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INTRODUCTION

Humans have had a negative impact on other animals for millennia (Barnosky et al., 2004) and, with the human population continuing to grow (Roser et al., 2013), wild animals may encounter humans with increasing frequency. Few wild animal species are unaffected by humans, and human activity undoubtedly creates huge and varied selection pressures (Sih et al., 2011).

Wild animals must avoid being hunted and persecuted, make foraging decisions in the presence of humans and select breeding sites in a human-dominated landscape. Additionally, habitat destruction can bring animals into close proximity to humans, where competition for food and space often leads to conflict (Pirta et al., 1997). As humans are a key driver of wildlife declines, understanding the behavioral and cognitive processes that shape wild animals' responses to humans is likely to be important in mitigating the detrimental effects of human activity. To successfully navigate encounters with humans, animals rely on a wide range of cognitive processes, as they must perceive and attend to relevant cues, integrate this information with previous experience, and mount the appropriate behavioral response (**Figure 1**).

While interactions between humans and domesticated animals have been relatively well-studied (e.g., Hare et al., 2002; Miklósi and Soproni, 2006; Proops and McComb, 2010; Nawroth et al., 2015), comparatively little research has focused on how free-living, wild animals respond to and interact with humans. Furthermore, as domesticated animals have been selected for docility and sociability toward humans (Wilkins et al., 2014; VonHoldt et al., 2017), the responses of such animals, even when feral, are likely to differ substantially from those of species with no evolutionary history of domestication. For instance, many wild species have a history of being hunted or persecuted, and avoidance of humans may be crucial for their survival. However, others have no such history and humans present a novel threat. Perhaps the best known case of human-mediated extinction in modern history is that of the dodo (*Raphus cucullatus*), whose naïveté to predators rendered the species vulnerable to exploitation by humans (Cheke, 2004). To this day, wild animals risk following the same fate (Ripple et al., 2019). Unless animals have the behavioral flexibility to accommodate anthropogenic change, it is likely that they will be disadvantaged (Lowry et al., 2013).

In this review, we consider human-wildlife interactions from the perspective of wild animals by examining how they perceive and respond to humans. We focus predominantly on studies of free-living animals and those brought into captivity temporarily for the purpose of study. Although animals raised in captivity can provide interesting insights into the potential cognitive abilities of their free-living counterparts, it is likely that extensive experience of humans modifies their behavior. We consider the cognitive challenge of discriminating between humans that pose differing levels of threat and responding appropriately. The factors that may drive individual differences in wild animals' responses to humans are also considered. The range of cues and the cognitive mechanisms that wild animals use to inform their responses to humans are not fully understood, and it is likely that humans affect animal behavior in ways that are not yet realized. We conclude by emphasizing the important role of animal cognition research in reducing human-wildlife conflict and improving conservation outcomes.

HOW DO WILD ANIMALS RESPOND TO HUMANS AS A SPECIES?

It is often unknown whether wild animals have evolved specific responses to humans, and whether flexible responses to humans

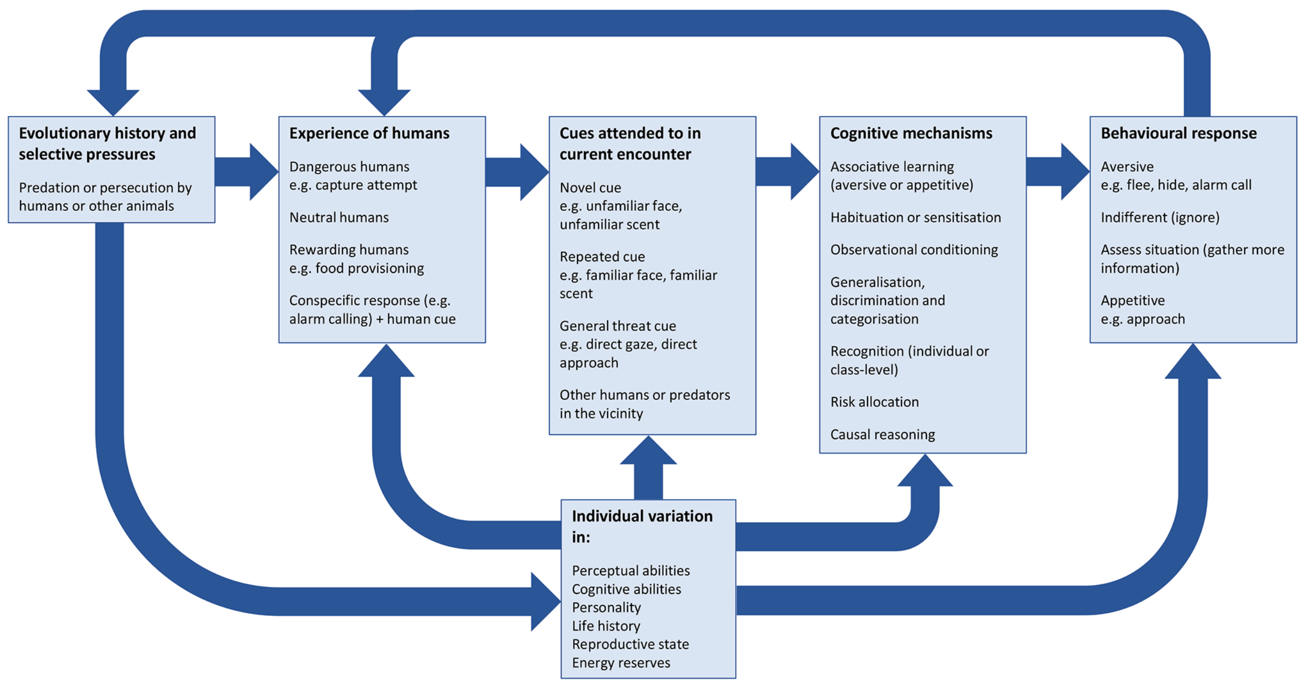

FIGURE 1 | Factors that may affect wild animals' behavioral responses during interactions with humans.

are human-specific. Humans may be seen in a similar way to other animals in the area, which could be as a predator or an insignificant part of the environment. While fear of humans may have a heritable component (Carrete et al., 2016), animals are able to learn to fear certain stimuli (though not all; Cook and Mineka, 1990). Understanding how wild animals perceive humans may help minimize wildlife disturbance and allow the implementation of more effective conservation strategies.

Studies of wild animals on islands that have been free of human activity throughout their evolutionary history show that, at least for some species, it may be difficult to learn to recognize novel predators such as humans. These islands also tend to be free of other large, terrestrial predators and, when predators are introduced, the naïve island species often lack an appropriate antipredator response (Sih et al., 2010). The vast majority of mammalian and avian extinctions in recent history have been island species (Johnson and Stattersfield, 1990; Ceballos and Brown, 1995), which may be due at least in part to their naïveté. Island species tolerate a closer approach by humans in comparison to closely related species in mainland areas, and the remoteness of islands further increases tolerance (Cooper et al., 2014). This is likely due to a historical lack of mammalian predators. For example, the Galápagos Islands have never been in contact with the mainland and large mammals have arrived only recently. Even after experiencing sustained chasing by a human, marine iguanas (*Amblyrhynchus cristatus*) did not show an increase of the stress hormone cortisol (Rödl et al., 2007). Additionally, while iguanas' heart rate increased upon seeing a native avian predator, they did not initiate a cardiovascular stress response at the sight of an approaching human, despite previously having experienced experimental capture (Vitousek et al., 2010).

Species that have evolved alongside large terrestrial predators indicate that wild animals may exhibit a generalized antipredator response and that current predation pressure may increase sensitivity to humans. For example, the presence of mammalian predators increases fear of humans in tammar wallabies (*Macropus eugenii*, Blumstein, 2002), and double-banded plovers (*Charadrius bicinctus*) flush sooner from humans in areas where domestic cats are present (St Clair et al., 2010). Predation pressure combined with non-predatory disturbance by humans may be sufficient to maintain antipredator responses to humans (Frid and Dill, 2002; **Figure 1**).

Wild animals that frequently encounter humans are likely to adjust their behavior in response to human disturbance. Animals may avoid areas where human disturbance is high (Dyer et al., 2001), but, if humans are not dangerous, they may remain in the area and habituate to human presence (Walker et al., 2006). In some cases, habituation to humans may produce negative consequences: for instance, there are concerns that great ape populations that are habituated to the presence of researchers may be more likely to enter croplands and come into conflict with local people (Hockings et al., 2015). Moreover, a decrease in escape response in areas where prolonged human disturbance occurs does not necessarily mean that animals perceive humans to be a lesser threat: animals may have little choice but to forage during times of high human disturbance and may adjust their responses according to temporal variation in human density, known as "risk allocation" (Lima and Bednekoff, 1999; Ferrari et al., 2009; Rodriguez-Prieto et al., 2009). Fear responses to humans are also affected by spatial variation in risk. For example, elk (*Cervus elaphus canadensis*) increase their vigilance in areas where hunting by humans occurs; this leads to a decrease in time spent feeding (Ciuti et al., 2012b). Some male red deer (*C. elaphus*) avoid hunting areas during the hunting season, despite these areas containing preferred forage, and ultimately have a better survival rate (Lone et al., 2015). Furthermore, a later study found that the feces of red and roe deer (*Capreolus capreolus*) contained higher stress hormone concentrations in areas where the main predators are humans rather than large carnivores (Zbyryt et al., 2018), indicating that these species perceive humans to be different from, and potentially more dangerous than, other predators. These studies highlight the trade-off many wild animals face between feeding and avoiding predation by humans, and the importance of making correct decisions about when and where to forage.

Human disturbance may have many long-term effects. If the presence of humans is stressful, this may be particularly problematic for species of conservation concern. Although some species habituate to human presence, others appear to become sensitized to it, with higher human disturbance causing an increase in stress responses. Even within groups of closely related species and when the nature of disturbance is similar, contrasting effects of human activity are evident. For example, while Magellanic penguins (*Spheniscus magellanicus*) exposed to tourism had lower stress hormone concentrations than their undisturbed counterparts (Walker et al., 2006), the opposite was true for yellow-eyed penguins (*Megadyptes antipodes*, Ellenberg et al., 2007). The stress induced by tourism resulted in lower reproductive success for the yellow-eyed penguins, a species already listed as endangered (Ellenberg et al., 2007). The apparent failure of some species to habituate to human presence is likely to be a key issue for conservation.

Responding to novel humans based on previous encounters with other humans requires some level of generalization of what was learned during these prior experiences: animals can only habituate to humans if they identify humans as being members of the same category, despite each human appearing different. Likewise, associations made during encounters with dangerous or rewarding humans are likely to influence later responses to humans (**Figure 1**). The degree to which wild animals generalize from their previous encounters, and their ability to discriminate between classes and individuals, depends on the cues that are attended to (see "Categorization of humans and class-level recognition" and "Individual recognition of humans").

Do Wild Animals Perceive Humans as Causal Agents?

The extent to which wild animals respond flexibly to humans may be influenced by their causal understanding of how humans interact with the environment. While responding to observable cues may often be sufficient, inferring that humans are capable of causing certain events may aid in modulating appropriate behavior. If wild animals are able to understand relationships between cause and effect, it may increase their ability to attend to relevant cues and ignore those that have no consequences. Evidence for an ability to recognize humans as causal agents has so far been controversial. Taylor et al. (2012) tested whether New Caledonian crows (*Corvus moneduloides*) differentiated between a stick that was moving because a human had entered a hidden location (a "hidden causal agent," or HCA) from which the stick emerged, and a stick that appeared to be moving without human intervention (an "unknown causal agent," or UCA). The stick was placed next to a feeder, such that crows could be hit if they fed while the stick was moving. The crows inspected the hole where the stick had come from less often, and were more inclined to feed, after the human had left the hide, while they were far more cautious after the UCA trials. The authors concluded that these results show that the crows were able to infer that the human caused the stick to move, and thus reasoned that it was safe to forage once the human had left the hide, while stick movement in the UCA trials was unpredictable. However, the authors presented all the crows with the HCA condition first, which means that the results might be confounded by increased test subject experience. This and other issues (see Boogert et al., 2013 and Dymond et al., 2013), mean that this result should be interpreted with caution.

In an experiment where North Island robins were given the choice of pilfering food in front of one of two humans, robins were more likely to avoid a human whose limbs were visible, a response that the authors suggest indicates reasoning about "capability" (Garland and Low, 2016). However, this trend was only observed when presented in combination with other modifications, such as stimulus size/shape and experimenter facial covering. Furthermore, if an understanding of capability is to be tested, the "incapable" human should be truly incapable of approaching the subject, and in such a way that is clearly observable. Despite these confounds, the general experimental setup seems suitable for tests of causal reasoning in habituated wild animals. A laboratory study with a similar design and sufficient controls indicated that captive chimpanzees (*Pan troglodytes*) were not able to reason about human limb capability: chimpanzees begged for food from humans who were physically unable to use their limbs to provide food, and did not learn over successive trials (Vonk and Subiaul, 2009). Although research on causal reasoning in non-human animals continues, there is currently little evidence that non-human animals have a robust understanding of the relationships between cause and effect (see Penn et al., 2008; Schloegl and Fischer, 2017 for reviews). It would be interesting to establish whether an inability to perceive humans as causal agents affects species' susceptibility to the negative effects of human activity.

THE NATURE OF HUMAN-WILDLIFE INTERACTIONS

Humans are an unusual species in that they can take a wide range of roles in their interactions with heterospecifics. Humans can present a unique challenge to wild animals, as different humans can pose different levels of threat: while many people ignore wild animals, some people kill them, and others actively feed them. Wild animals that live alongside humans would benefit from being able to discriminate between humans taking these vastly different roles (**Figure 1**). Here, we describe how the different roles that humans take affect animal behavior, before considering the cognitive mechanisms that potentially allow wild animals to overcome the challenge of distinguishing between them.

Dangerous Humans

Humans pose a threat to wild animals for a range of reasons. Humans may act as predators, killing animals for food (Ripple et al., 2015), sport (Loveridge et al., 2007), or even for conservation purposes (Russell et al., 2016). They may also act as competitors and kill animals to prevent or reduce consumption or damage of resources. Large carnivores such as lions (*Panthera leo*) are often killed to prevent predation of domesticated animals (Woodroffe and Frank, 2005), while herbivorous mammals and birds are commonly targeted for consuming crops (Gebhardt et al., 2011; Ango et al., 2017). Animals targeted by lethal practices may benefit from showing heightened fear of humans. For example, an experimental study found that black-billed magpies (*Pica hudsonia*) flew away sooner from an approaching human in rural agricultural areas, where they are persecuted, than in rural parks, where they face no such persecution (Kenney and Knight, 1992). A long-term study found that coyotes (*Canis latrans*) became more active during the daytime after intense persecution from humans had ended (Kitchen et al., 2000), and a recent meta-analysis indicated that mammals in areas of high human disturbance have become more nocturnal compared with conspecifics in areas where human disturbance is lower (Gaynor et al., 2018). The type of persecution animals face also appears to be important: crows (*Corvus macrorhynchos* and *Corvus corone*) are more wary of humans in areas where they are shot rather than cage-trapped, perhaps because associations between humans and dead conspecifics are formed more easily in the former case (Fujioka, 2020). A particularly striking example of how wild animals might learn to evade human predation comes from Diana monkeys (*Cercopithecus diana*), which usually respond to predators by alarm calling and approaching. Human hunters have taken advantage of this by imitating calls of predators and distressed prey. Monkeys in areas where poaching occurs have an increased ability to distinguish between imitations by humans and real alarm calls, and subsequently call less, compared to monkeys in areas where there is no poaching (Bshary, 2001). These studies indicate that individuals of targeted species are able to respond flexibly to direct threats posed by humans. Moreover, these examples show how human perceptions and differences in cultural practices can ultimately shape wild animal behavior.

Neutral Humans

Many humans present no direct threat to wild animals. A neutral human will either ignore wild animals or observe them from afar, and will not interfere with their behavior. An example of a neutral human could be someone who allows wild animals to live close by without either deterring or encouraging them. If an animal only ever encounters neutral humans, they are likely to exhibit behavior that differs from that of animals with experience of dangerous humans. Responding aversively to humans that do not present a threat is suboptimal as it is likely to entail unnecessary energetic costs and reduced feeding time (Ydenberg and Dill, 1986). Animal populations that experience high human disturbance, such as those in urban areas, are often more tolerant of humans than are those in areas of lower human disturbance (Samia et al., 2015). This could be a result of habituation to repeated non-threatening encounters, or reflect population-level differences in tolerance that enable certain individuals to settle in areas where they will be frequently disturbed (Blumstein, 2016).

Of course, humans can intend to be neutral but their behavior could have unintentional consequences that create positive or negative outcomes for wild animals, e.g., through accidentally dropping food or littering. Additionally, whether or not wild animals make aversive or appetitive associations with humans in general can be out of an individual human's control. As animals are able to associate events with neutral environmental stimuli (Cassens et al., 1980), wild animals may perceive humans as "dangerous" or "rewarding" irrespective of whether that human caused a particular outcome. How animals view neutral humans may also be affected by their previous experiences with other people, and the extent to which they generalize or discriminate between individual humans.

Rewarding Humans

Although many interactions with humans appear to be neutral or negative from the perspective of wild animals, interacting with humans can also be advantageous. Many humans purposefully provide care to wild animals, including through direct feeding interactions (Marion et al., 2008). While such close contact can carry a risk of harm to both humans and wild animals (e.g., from disease and aggression; Orams, 2002), such interactions provide at least short-term benefits and often result in attraction to humans (Sabbatini et al., 2006; Donaldson et al., 2010). Humans also provide food indirectly, for example by accidentally dropping food during picnics, and may thus be associated with reward (Marion et al., 2008). Relatively little research has focused on the effects of "rewarding" humans on wild animal behavior. However, risk-sensitive foraging theory predicts that the cost of failing to respond appropriately to humans in dangerous roles (i.e., by fleeing or hiding) would outweigh the benefits of being attracted to humans in a rewarding role: even if the risk of being killed is low, the risk of starving from a lack of extra food is likely to be far lower (McNamara and Houston, 1992).

It is even possible for humans to have a mutualistic relationship with wild animals, where both parties gain measurably from the interaction. In parts of Africa, for example, humans forage for honey alongside greater honeyguides (*Indicator indicator*), which feed on bees' wax and larvae. These brood-parasitic birds are unable to access bees' nests and actively solicit human cooperation (Isack and Reyer, 1989). Honey hunters can also attract a honeyguide by making a specific call (Isack and Reyer, 1989). As honey hunters report that juvenile honeyguides, which are raised by other species, initiate foraging trips, it is likely that this relationship has evolved through selection (Spottiswoode et al., 2016). The observation that they do this before responding to the call indicates that there is also likely to be an important role for learning, particularly as honeyguides respond to the specific calls of the honey hunters in their local area (Spottiswoode et al., 2016). Whether honeyguides learn these calls through individual experience or socially from the responses of conspecifics is currently unknown. It is plausible that a honeyguide could learn to associate a honey-hunting call with the subsequent reward of food if honey hunters call while following the honeyguide to the bee's nest. Examples such as this exemplify why some wild animals benefit from being attracted to human cues.

HOW DO WILD ANIMALS DISTINGUISH BETWEEN DANGEROUS AND NEUTRAL HUMANS?

Animals may respond differently to different groups of humans and exhibit a specific response only to humans displaying a particular cue, such as a distinctive item of clothing (e.g., Bates et al., 2007). If only a certain behavior or type of human represents a threat, animals will benefit from attending to these cues rather than those of neutral humans (**Figure 1**). Animals may respond to cues that are threatening regardless of the species displaying them if they are intrinsically associated with negative outcomes; these cues may or may not require learning. Examples of such general threat cues that affect wild animals' behavior include direct gaze (discussed below), direct approach (Burger and Gochfeld, 1981), and a fast approach speed (Cooper et al., 2003). Wild animals may also learn to attend to cues that are specific to humans. Here we discuss cues that have been well-studied, but there are potentially many different types of cue that animals could use to inform their responses.

Gaze Direction

Animals may use the direction of human gaze to identify and avoid dangerous humans. Gaze direction is an indication of where attention is directed, and human gaze direction is likely to be particularly discernible as humans have forward-facing eyes. Additionally, humans have visible white sclerae which, contrasted against the darker irises, potentially make the direction of their gaze more conspicuous than that of other mammals (Kobayashi and Kohshima, 1997). Gaze aversion, whereby animals exhibit a fearful response to another's eye direction, appears to be taxonomically widespread among vertebrates and likely functions as a means of avoiding predation and altercations with competitors (see Davidson et al., 2014; Davidson and Clayton, 2016 for reviews of gaze sensitivity). Using gaze direction as a cue should enable animals to attend to dangerous or aggressive individuals in the environment while ignoring those that do not pose a threat. Indeed, wild animals of a wide range of species respond differently when a human is looking at them compared to looking away; they typically flee sooner (e.g., Burger et al., 1992; Eason et al., 2006; Bateman and Fleming, 2011; Clucas et al., 2013; Cooper and Sherbrooke, 2015), or take longer to approach food (Carter et al., 2008; Garland et al., 2014; Goumas et al., 2019) or their nests (Watve et al., 2002) when exposed to direct human gaze.

Animals may not necessarily respond aversively to human gaze in all contexts. Being approached by a human could be perceived as a predation attempt, whereas a human sitting passively while directing their gaze at an animal may have no such connotations. It may even be possible for wild animals to come to associate direct human gaze with reward. In cases of wildlife feeding, for example around duck ponds, human gaze may be appetitive rather than aversive, as a human is likely to direct food toward an individual it is looking at. However, to our knowledge, there has been no research on whether wild animals respond appetitively to human gaze. Interestingly, in a study of hand-raised, captive jackdaws, von Bayern and Emery (2009) found that test subjects only responded aversively to human gaze, measured by latency to retrieve food, when the human was unfamiliar to them. Whether free-living animals adjust their behavior in this manner has not been tested.

Gaze aversion experiments have not always distinguished between head direction and eye direction, but a response to head direction is not necessarily indicative of a reaction to eyes. In humans and other predators, head direction may be a good proxy for eye direction, and is potentially more salient, and therefore may be a useful cue for wild animals to use. However, using a cue that is only sometimes informative is not optimal. Hampton (1994) showed that captive house sparrows (*Passer domesticus*) attempted to escape most often when his head was facing them rather than turned away, regardless of eye direction. Some studies have found that several other passerine species do appear to pay attention to eyes specifically (American robins *Turdus migratorius*, Eason et al., 2006; European starlings *Sturnus vulgaris*, Carter et al., 2008; American crows *Corvus brachyrhynchos*, Clucas et al., 2013; North Island robins *Petroica longipes*, Garland et al., 2014).

Responses to eye direction invoke the question of whether wild animals have the ability to take another's perspective. If animals are able to understand that other individuals have a different viewpoint, they may be able to better predict their behavior. Do animals that exhibit aversion to direct gaze understand that they are being watched? It could certainly explain why these individuals are fearful, but a "Theory of Mind" explanation is not necessary to account for the observed behavior, if, for example, eyes are inherently aversive or animals learn to associate direct gaze with a predation attempt. Studies where the experimenters direct their attention toward an object, rather than the test subject (e.g., Carter et al., 2008), suggest that wild animals of some species may not simply be reacting to the presence of eyes and are instead able to follow human gaze. This has been demonstrated in captive corvids and primates (e.g., common ravens *Corvus corax*, Bugnyar et al., 2004; gibbons *Hylobates* spp. Liebal and Kaminski, 2012).

While laboratory experiments indicate that corvids can take the perspective of conspecifics and may thus have a Theory of Mind (Dally et al., 2010; Bugnyar et al., 2016), very few studies have attempted to address the question of whether free-living wild animals understand the perspective of a human observer. Watve et al. (2002) devised an experiment that made use of visual barriers near the nests of green bee-eaters (*Merops orientalis*). The experimenter could take one of two positions when the focal bird was on a nearby perch, ready to enter the nest to feed its chicks. In one position, the experimenter could see the bird but not the nest; in the other, both could be seen. The bee-eaters made more visits to the nests and had a shorter approach latency when the experimenter's view of the nest was obstructed, implying that the birds were not simply reacting to their view of the experimenter. However, the experimenter was looking at the bird rather than the nest. It is therefore unclear whether the bee-eaters were simply reacting to the experimenter watching them as they approached the nest, and were deterred by direct gaze. Stronger evidence for perspective-taking might be provided by a study where the experimenter measures the bird's latency to leave the perch before entering the nest, while keeping their gaze directed at the nest.

The widespread nature, early-life presence and clear utility of gaze aversion have led to the assumption that such responses to gaze are "innate" (Coss, 1979; Shepherd, 2010). We interpret "innate" in this context to mean that animals do not require prior experience of gaze stimuli in order for gaze aversion to manifest. Although this may be a parsimonious explanation for its documented presence in several vertebrate classes, few studies have actually attempted to address this question. While several species show aversive responses to two horizontally-positioned eye-like stimuli early in development (ray-finned fishes: Coss, 1978; Altbäcker and Csányi, 1990; Miklósi et al., 1995; chickens *Gallus gallus*: Scaife, 1976; Jones, 1980), whether or not experience is required to mediate these responses is unclear and may be species-specific. For example, jewel fish (*Hemichromis bimaculatus*) that were deprived of seeing eyes or eye-like stimuli during early life showed an aversive response to two horizontal eye spots, whereas fish that were raised in the presence of conspecifics did not (Coss, 1979). Conversely, bobwhite quails (*Colinus virginianus*) raised without exposure to human faces tended to ignore the direction of human gaze, whereas those previously exposed to them avoided areas where a human was looking (Jaime et al., 2009). Without further studies that begin at birth or hatching, and control for exposure to all eyes or eye-like stimuli, it is impossible to conclude that gaze aversion is innate. There is some evidence that attention to eyes or eye-like stimuli may be innate by our definition (see e.g., Batki et al., 2000; Sewards and Sewards, 2002 for evidence from human neonates and other amniotes), and this may facilitate early development of gaze aversion. An evolved mechanism for attending to eye-like stimuli, and an ability to learn quickly, would provide animals with the capacity to use gaze cues without the need for perspective-taking.

Categorization of Humans and Class-Level Recognition

The ability to categorize humans into groups based on shared features may allow animals to respond appropriately according to the risk associated with different groups. This is likely to be particularly important in areas where different groups of people pose different levels of threat. For example, the same area might be inhabited by some groups of people who commonly engage in hunting or kill wild animals to protect resources, while other people may not pose a threat. To categorize a human usefully, an animal must be able to discriminate between different classes of humans by attending to relevant cues, shared only by members of a single class, and ignoring uninformative cues. Distinguishing between dangerous and neutral classes of humans is likely to occur through associative learning, whereby animals associate the cue with an aversive action. Being able to recognize a member of a class ("class-level recognition") requires that animals remember the cue and its association in later encounters.

Wild animals' ability to categorize humans according to the level of threat they pose is beautifully illustrated by a series of experiments conducted in Amboseli National Park in Kenya. There, African elephants (*Loxodonta africana*) compete with domesticated animals for food and water and occasionally kill humans (Browne-Nuñez, 2011). This creates conflict with Maasai pastoralists, who spear elephants in retaliation (Browne-Nuñez, 2011). In contrast, the sympatric Kamba people pose relatively little threat to elephants (Bates et al., 2007). In an experiment to test whether elephants in Amboseli differentiate between the two groups of people, Bates et al. (2007) exposed free-living elephants to garments that had been worn by Maasai and Kamba men and assessed whether the scent of the garments affected their behavior. They also tested whether elephants could use visual cues to identify groups: Maasai people typically wear distinctive red clothing so the researchers measured elephants' reactions to red vs. white unworn cloths. Elephants directed aggressive displays toward the red cloth at a higher frequency than they did towards the white cloth. They also moved faster and further away from Maasai-worn cloth than Kamba-worn cloth upon detecting the scent. Furthermore, the elephants responded similarly to the Maasai-worn cloth whether or not they had individual experience of being hunted by Maasai men, which indicates that elephants' responses to threatening cues can be facilitated by social learning.

A subsequent experiment by McComb et al. (2014) tested elephants' ability to differentiate between Maasai and Kamba people based on the sound of their voices. The researchers used playbacks of Maasai and Kamba men speaking the same words in their respective languages. The elephants were more likely to spend time sniffing and bunching up closely together (a defensive behavior) when they heard a Maasai man's voice compared to a Kamba man's voice. Additionally, elephants were more likely to retreat from the voices of Maasai men than those of Maasai women or boys: Maasai women and boys pose little threat to elephants. The elephants still responded with defensive behavior more frequently to the men's voices than the women's voices even after the pitch had been altered to resemble that of the opposite sex, suggesting that the acoustic cues they use to differentiate Maasai men from other groups are very subtle. Together, these experiments demonstrate that elephants can discriminate between threatening and non-threatening groups of people based on visual, olfactory and acoustic cues.

Visual cues may be particularly useful for wild animals being hunted, as hunters are likely to minimize the amount of sound they make. For example, a study of Poeppig's woolly monkeys (*Lagothrix poeppigii*) in the Ecuadorian Amazon indicated that hunting pressure may affect this species' responses to humans carrying objects and displaying behavior associated with danger (Papworth et al., 2013). Researchers simulated the appearance and behavior of individuals from groups of people that monkeys in the area were likely to have encountered previously: hunters, who regularly kill monkeys; gatherers, who collect resources on the ground and pose little threat to monkeys; and researchers, who usually passively observe monkeys. Observers recorded the change in behavior of the monkeys after detecting humans acting in each experimental condition and compared sites where monkeys were known to face low and high hunting pressure. In response to seeing a "hunter," monkeys at both sites made fewer vocalizations, reduced their visibility and moved away, whereas their responses to the other conditions were mixed. While this experiment does not allow conclusions to be drawn about whether it is human behavior, objects, or the combination of these cues that are important in affecting woolly monkey behavior, it adds to the evidence that free-living animals may be able to distinguish dangerous from non-dangerous groups of people based on classifiable visual cues. Future research that assesses the relative importance of human behavior and associated objects would increase our understanding of the cues that wild animals use to infer the level of risk posed by different groups of people.

INDIVIDUAL RECOGNITION OF HUMANS

While being able to classify humans into groups may be an effective way to evade danger, it will not always be possible to group humans usefully. Humans that may appear very similar can act very differently. In places where wild animals repeatedly encounter humans that exhibit consistent inter-individual differences in the level of threat they present, being able to accurately identify individual humans would facilitate avoiding risky encounters with dangerous individuals (**Figure 1**). Conversely, responding fearfully to humans that do not present a threat may lead to reduced feeding opportunities and increased movement, both of which would incur an energetic cost (Ydenberg and Dill, 1986); therefore, responding appropriately to those people who are known to be threatening or rewarding could be advantageous.

In order to recognize an individual, an animal must first be able to discriminate between members of a species, subsequently remember the individual's features and then match the cues stored in its memory with the observed cues of the individual at a later time (Tibbetts and Dale, 2007).

Many animals appear to be able to distinguish between members of their own species, which should be beneficial in social interactions such as pair-bonding (Jouventin et al., 2007), attending to offspring (Beecher et al., 1981) and defending territories from unfamiliar intruders (Molles and Vehrencamp, 2001). If animals are able to discriminate between conspecifics, the same cognitive processes may also enable them to discriminate between heterospecifics, such as humans.

Several studies have tested whether wild animals can recognize individual humans. One of the first was conducted on northern mockingbirds (*Mimus polyglottos*): in the experiment, a human repeatedly approached and touched a mockingbird's nest, thus presenting a salient threat (Levey et al., 2009). Mockingbirds responded to successive approaches by flushing earlier, increasing alarm calling and attacking the intruder. In contrast, their responses to a novel intruder did not differ from those they made in response to the original intruder on their first encounter.

Which features do wild animals use to differentiate between individual humans? Subsequent studies on other bird species have used masks to standardize the appearances of faces and test for discrimination of facial features (Marzluff et al., 2010; Davidson et al., 2015). This may be particularly important in recognizing individual humans, as humans may change their clothing and hairstyles on a frequent basis. Indeed, humans heavily rely on facial features to recognize each other (Maurer et al., 2007). Experiments that used masks to test individual human recognition in free-living American crows have indicated that facial features are important cues in identifying dangerous humans (Marzluff et al., 2010). Interestingly, although crows scolded masks that had been worn during their capture more than they did previously unseen masks, crows also mobbed a person wearing a hat previously paired with a "dangerous" mask in the absence of that mask, suggesting that crows may sometimes use more conspicuous, but changeable, cues rather than identify individual faces.

In another study, American crows were brought into captivity to assess the neural circuitry underlying their responses to familiar human faces (Marzluff et al., 2012). The crows were exposed to one of three stimuli: a human wearing a "threatening" mask that had been worn during the test subjects' capture, a human wearing a "caring" mask that had been worn while feeding the crows while they were in captivity, and an empty room as a control. Positron emission tomography revealed that the sight of both of the masks activated the rostral forebrain, an area associated with memory and learning (Marzluff et al., 2012). Parts of the amygdala and thalamus, areas associated with fear, were activated more strongly at the sight of the threatening mask than the caring mask. A follow-up experiment that used a human wearing a novel mask as a stimulus, either empty-handed or holding a dead crow, found that certain brain areas, such as the hippocampus and optic tectum, were more strongly activated at the sight of the person with the dead crow, which may facilitate learning of danger (Cross et al., 2013). However, additional control conditions are necessary to determine to what extent the sight of a dead crow itself triggers specific neural activity independent of human presence.

Most of the studies testing individual recognition of humans by wild animals have focused on birds, particularly members of the Corvidae (e.g., Marzluff et al., 2010; Lee et al., 2011; Davidson et al., 2015), a family often described as "feathered apes" because of their comparatively large brains (Emery, 2004; Lambert et al., 2019). However, a study of feral pigeons (*Columbia livia*) in an urban park indicated that this species may also have the ability to recognize individual humans (Belguermi et al., 2011). The experimenters counted the number of pigeons feeding next to a "hostile" and "friendly" human, where the hostile human had interrupted and chased away pigeons in the training sessions, while the friendly human had kept still and allowed the pigeons to feed. Pigeons discriminated between the "hostile" and "friendly" human, even when the experimenters switched locations and coats, suggesting that pigeons may have been using facial cues. If so, this would show that corvids are not unique among birds in recognizing human facial features. This may not be surprising considering the results of a study on honeybees (*Apis mellifera*), which found that these insects were able to discriminate between images of different humans' faces, and later recognized the target face with a high degree of accuracy (Dyer et al., 2005). This indicates that a capacity to learn human facial features is not limited to the comparatively large and complex brains of vertebrates.

It may be expected that only species or populations that have historically been in regular contact with humans would have an ability to recognize individual humans. A study of Antarctic skuas (*Stercorarius antarcticus*) suggests that this may not be the case (Lee et al., 2016). Skuas on King George Island, which has been colonized by humans only relatively recently, were repeatedly approached at their nests by one of two "intruders." On the fourth visit, the intruder was joined by a neutral human, whom the skuas had not seen before, and both wore identical clothes. The experimenters walked in opposite directions away from the nest and recorded which person the skuas followed. All seven skua pairs tested chased after and attacked the intruder rather than the neutral human. This study shows that an evolutionary history of living alongside humans does not appear to be necessary for discrimination of individuals, and suggests that the ability to recognize individual humans could be a general ability originating from a need to recognize individual conspecifics. However, it remains to be shown whether wild animals that are completely naïve to humans would be able to discriminate between individuals.

A study of house sparrows provides evidence that the ability to recognize individual people may not arise from extensive experience with humans (Vincze et al., 2015). Subjects were brought into captivity from the wild, from locations designated "urban" and "rural" according to human population density. They were then exposed to an experimenter wearing different masks. The "hostile" mask was paired with a simulated attack from behind the bars of their cages, while the "non-hostile" mask was worn for encounters where the experimenter stayed still in front of the cage. An unfamiliar mask was also used in the test trials, where the sparrows' risk-taking behavior in response to each mask was quantified. Contrary to the authors' expectations, sparrows from rural but not urban locations showed a difference in response to the hostile and non-hostile masks, with rural sparrows taking more risks in the presence of the non-hostile mask. While this finding might suggest that urban sparrows do not have the ability to recognize individual humans, it may more likely be a result of other factors such as a difference in boldness, particularly as rural sparrows were more risk-averse than urban sparrows when exposed to the unfamiliar mask. It is therefore important to consider variation among subjects when studying their responses to human cues (see "Variation in responses to humans").

"True" Individual Recognition?

What may appear to be individual recognition, i.e., discrimination and memory of an individual's unique cues, could result from discrimination at the class level (as described in the previous section). For example, a parent may recognize their offspring as their own, but not be able to distinguish among members of their litter or clutch. Similarly, a wild animal may distinguish between a choice of two humans, but not from a wider selection of humans. If subjects respond to only one of the individuals featured in the experiment, it is unknown whether the subjects are responding to the individual rather than a particular cue or set of cues that may be shared by other individuals that exist outside the experimental setup (see e.g., Tibbetts and Dale, 2007; Proops et al., 2009).

To find out whether animals are responding to specific individuals, rather than exhibiting a generalized response to a group of individuals with shared or similar features, some researchers have recommended testing whether animals integrate cues from different sensory modalities, such as visual and auditory cues (Proops et al., 2009; Yorzinski, 2017). In studies of cross-modal recognition, a cue associated with one individual in one sensory mode (e.g., the sight of a familiar individual's face) is paired with a cue of another individual in a different sensory mode (e.g., a different individual's voice) to create an "incongruent" stimulus. Animals that are able to integrate both types of cue to form a mental representation of an individual are expected to show signs of expectancy violation when cues from two different individuals are presented together. Therefore, animals may look longer at the incongruent stimulus compared to a congruent stimulus consisting of two cues from the same individual. Such behavior indicates that the subject has an internal representation of the individual and thus recognition must be at the individual rather than class level. The cross-modal experimental paradigm has been used to show individual recognition of conspecifics by free-living African lions (visual-auditory, Gilfillan et al., 2016), but whether wild animals could cross-modally recognize individual humans remains unknown. As it requires animals to be familiar enough with individual humans to recognize them with more than one sense, it may not be likely.

The converse of the problem of whether animals are truly recognizing individuals, rather than classes, is whether a lack of appropriate behavioral response is truly indicative of an inability to discriminate between individuals. An animal may be able to perceive and remember differences between individual humans, but generalize an encounter with one human to all or a wider set of humans. As yet, the conditions under which wild animals generalize from encounters with humans are unknown. The number of previous encounters with humans, the number of different humans encountered and their perceptual similarity could potentially affect how animals respond to an unfamiliar human. This may be particularly important in understanding the effects of feeding interactions. If animals generalize from their experiences of being given food by rewarding humans, they may be more inclined to approach unfamiliar humans and be at risk of being harmed by dangerous humans. Research in this area would therefore be valuable.

Social Learning About Dangerous Individual Humans

In many species, information about danger can spread through a population by social learning, often through observational conditioning (Griffin, 2004). This can be facilitated by exposure to conspecific alarm calling and mobbing the threatening stimulus, usually a predator. Alarm calls function to alert other individuals in the vicinity to danger, and alarm calling can cause an otherwise innocuous stimulus to be perceived as a threat (Curio et al., 1978). Following up on the finding by Marzluff et al. (2010) that American crows remember people that have previously captured them, Cornell et al. (2011) tested whether this information subsequently spreads to conspecifics. They found that, even 5 years after the capture event, crows continued to scold the dangerous mask to a greater extent than the neutral mask. The increasing number of crows scolding over time, combined with scolding by lone crows that had never been captured, indicated that the stimulus had been learned socially *via* observational conditioning, with the sight and sound of conspecifics scolding allowing naïve crows to learn the association. A study of another corvid, the Eurasian jackdaw (*Corvus monedula*), found that just the sound of conspecifics scolding was sufficient to cause a change in behavior toward a human wearing a particular mask (Lee et al., 2019): jackdaws returned to their nest-boxes more quickly when confronted with the "scolding" mask compared to a previously-seen neutral mask. These experiments highlight the potential benefit of learning the cues of individual humans through social means: a subject need not experience a dangerous encounter with a human in order to learn to avoid the same human in later encounters, which could have considerable implications for survival.

VARIATION IN RESPONSES TO HUMANS

In the previous sections, we outlined how cognitive processes influence the responses of wild animals to encounters with humans. However, not all animals respond to humans in the same way, and considerable variation exists both between and within species. Understanding the causes and consequences of this variation is important, as it may influence the ability of animals to persist in habitats dominated by anthropogenic activity (Sih et al., 2011; Lowry et al., 2013; Sol et al., 2013).

In this section, we discuss how wild animals vary in their responses to humans, the proximate mechanisms underlying this variation, and its wider ecological implications. We then outline how an understanding of the cognitive processes underlying responses to humans, and the interactions of these processes with other traits, can be applied to help address urgent conservation and wildlife management problems.

Why Do Animals Vary in Their Responses to Humans?

Variation in responses to humans may arise if animals differ in their perception of cues, their previous experience and/or their behavioral decision-making processes (Sih et al., 2011; see previous sections). Variation can arise at each of these stages: for example, while animals may perceive relevant cues and classify them in a similar way, differences in prior experience may result in behavioral variation (Sih et al., 2011; Greggor et al., 2014, 2019). Firstly, an animal's response to a cue is likely to depend on the specificity of the cue itself, and how reliably it predicts a particular outcome (Shettleworth, 2010). The animal's subsequent behavioral response may then be based on the context-specific payoff of potential outcomes; for instance, animals may decide to ignore a cue signaling a mild threat if fleeing incurs a substantial energy cost (Sih et al., 2011). Responses to novel cues may further depend on how closely cues match those encountered in an animal's evolutionary past or previous experience, which may have generated a cognitive or perceptual bias for certain types of information. For example, wild animals may be more likely to attend to human gaze cues if they frequently attend to the gaze direction of conspecifics (see Davidson et al., 2014 for a discussion), or they may employ social learning to avoid dangerous people if they rely heavily on social learning in other contexts. Additionally, individual-level factors such as personality, response to novelty, reproductive state and previous experience also influence how individuals use information from their environment (Sih and Del Giudice, 2012; Greggor et al., 2017, 2019; **Figure 1**), and are therefore likely to contribute to decision-making during encounters with people. Although there is growing interest in how cognitive variation influences responses to human-induced rapid environmental change in general (e.g., Greggor et al., 2014, 2019; Barrett et al., 2019), relatively few studies have focused specifically on the role of cognition in determining how animals respond to humans themselves.

To date, the majority of studies investigating behavior during human-wildlife encounters has focused on quantifying differences between animal populations in habitats that differ in the level of human disturbance, such as along urban-rural gradients (e.g., Samia et al., 2015; Gaynor et al., 2018; Breck et al., 2019). While animals living in urban habitats are typically less fearful of humans than their rural counterparts, the mechanisms driving this variation remain relatively poorly understood (Sol et al., 2013). It is possible that urban environments select for individuals with particular traits that enhance survival and reproductive success (natural selection), or that individuals with certain traits are more likely to colonize urban habitats in the first place (non-random sorting). Perhaps the more common (though not mutually exclusive) scenario is that animals living in urban environments adjust their behavior over time *via* learning, or other forms of behavioral plasticity (Sol et al., 2013). These behavioral adjustments may take many forms, including altering habitat use to minimize contact with people (Duarte et al., 2011; Bonnot et al., 2020), or becoming more tolerant of human presence through habituation and/or risk allocation (Lima and Bednekoff, 1999; Rodriguez-Prieto et al., 2009). Whether animals tolerate or avoid human disturbance is likely to depend on the nature of their interactions with people. For example, eastern gray kangaroos (*Macropus giganteus*) flee more readily from humans in areas with higher hunting pressure, compared to those in areas with a higher density of tourists and other forms of non-lethal disturbance (Austin and Ramp, 2019). Conversely, animals may approach humans in areas where this behavior is actively rewarded: Barbary macaques (*Macaca sylvanus*) appear to spend more time using roadside habitat where they are provisioned by tourists, especially at times of higher tourist activity and when natural food sources become scarce (Waterman et al., 2019). Currently, most studies in this area focus on how animals make escape decisions during encounters with humans. As a result, less is known about how animals come to associate people with reward as opposed to danger. In areas where wild animals encounter humans that vary in their level of threat, animals may benefit from using human cues to assess risk, categorizing people based on risk level, and discriminating between individual humans (see previous sections).

Even within the same habitat, individuals may differ in their behavior during encounters with humans. For example, burrowing owls (*Athene cunicularia*) show individual consistency in flight initiation distance (Carrete and Tella, 2013), roe deer react in a moderately repeatable way to capture and handling (Bonnot et al., 2015), and yellow-bellied marmots (*Marmota flaviventris*) differ in their rates of habituation to humans (Runyan and Blumstein, 2004). While an individual's previous experience is likely to inform their decision-making, personality differences may also contribute to the observed variation in responses. Personality, which refers to consistent inter-individual differences in behavior, is widespread in the animal kingdom (Bell et al., 2009; Sih et al., 2012). These behavioral differences influence animals' responses to novel resources or habitats (e.g., Kozlovsky et al., 2017; Lapiedra et al., 2017; Thompson et al., 2018; Breck et al., 2019) and novel threats (Short and Petren, 2008; Lapiedra et al., 2018). Suites of behaviors may be correlated across contexts in a behavioral syndrome (Sih et al., 2004), potentially influencing how individuals respond to ecological change (Dingemanse et al., 2004; Sih et al., 2012; Lapiedra et al., 2017).

Individuals may also differ in how they gather and process information during decision-making; while explaining inter-individual differences in cognitive ability is a topic of growing research interest (Boogert et al., 2018; Cauchoix et al., 2018), it is not known how cognitive variation influences behavior during human-wildlife encounters. Furthermore, it is highly likely that personality interacts with cognition to determine how individuals respond to humans. For example, individuals' exploratory tendencies may influence their exposure to cues in the environment, and also opportunities for learning (Sih and Del Giudice, 2012). While intriguing, the relationship between personality and cognitive ability is currently poorly understood and is likely to be complex, potentially varying between populations and habitats in a context-dependent manner (Dougherty and Guillette, 2018). Regardless of the exact mechanisms involved, the fact that individuals appear to differ in their responses to human encounters raises the possibility that some individuals may be better able to cope with the challenge of living alongside humans. If these behavioral differences are heritable and enhance fitness, this could result in long-term evolutionary change (Sol et al., 2013).

Though empirical studies are currently limited, there is some evidence to suggest that animals' responses to human disturbance may influence survival and reproductive success. For example, elk and brown bear (*Ursus arctos*) show consistent individual differences in their tolerance of human disturbance, which influences habitat use during the hunting season; consequently, individuals that spend more time near roads are more frequently seen and killed by hunters (Ciuti et al., 2012a; Leclerc et al., 2019). A study of spotted hyenas (*Crocuta crocuta*) also suggests that individuals that take more risks when foraging are less likely to survive to adulthood (Greenberg and Holekamp, 2017); in this case, responses to humans were not investigated explicitly, but the findings indicate that differences in risk-taking tendencies may have important implications for survival in anthropogenic habitats. These examples illustrate how humans, through our lethal and non-lethal interactions with wildlife, may exert selective pressure on cognition and behavior. While the mechanisms underpinning animals' responses to humans are not well understood, their impacts have potentially far-reaching consequences for evolutionary processes and population dynamics, as discussed in the next section.

Wider Implications

Although human activity has been shown to exert strong selective pressure on wildlife (Hendry et al., 2008; Darimont et al., 2009), how direct encounters with humans shape animal cognition and behavior is poorly understood. Identifying the factors that influence animal decision-making, and their fitness consequences, may shed light on why some species (or individuals) are more successful than others in exploiting human-dominated habitats. In particular, we can begin to determine: (i) the extent to which individuals change their responses to humans within their lifetime, and the cognitive processes involved (plasticity), (ii) whether individual variation in human-disturbed habitats reflects the behavioral variation at the species level, or whether these individuals represent a "subset" of the population (non-random sorting), and (iii) the extent to which these behaviors are heritable, and contribute to individual fitness (natural selection; Sol et al., 2013). Furthermore, we can begin to investigate how these processes interact with factors such as life history to influence population persistence (Sol et al., 2013; Maspons et al., 2019). How behavior and life history interact to influence survival in changing environments is not well understood, but current evidence suggests that the value of behavioral plasticity may be higher for species with long lifespans and comparatively low rates of reproduction (Maspons et al., 2019). Thus, processes such as learning could buffer populations against the effects of maladaptation and enhance survival under rapidly-changing conditions (Maspons et al., 2019).

In addition to influencing species persistence, how wild animals respond to encounters with humans may affect population dynamics and community composition (Schlesinger et al., 2008; Tuomainen and Candolin, 2011; Pirotta et al., 2018). For example, the extent to which animals tolerate or avoid humans is likely to influence habitat use (Rodríguez-Prieto and Fernández-Juricic, 2005; Mallord et al., 2007), leading to local changes in species abundance and richness (Mallord et al., 2007; Bötsch et al., 2017, 2018). As a result, these changes may modify interactions between predators and prey (e.g., Berger, 2007; Gaynor et al., 2018; Bonnot et al., 2020). Changes in predator-prey interactions may have wider population-level impacts: for instance, puma (*Puma concolor*) respond to human disturbance by reducing feeding time at individual kills, but appear to compensate for this reduced energy intake by killing more deer in areas of higher human population density (Smith et al., 2015). How wild animals respond to encounters with humans may therefore not only influence individual fitness, but the composition and persistence of entire communities, with implications for conservation and the mitigation of human-wildlife conflict.

CONSERVATION AND MANAGEMENT APPLICATIONS

A clearer understanding of how animals respond to encounters with humans could be applied to mitigate the impacts of anthropogenic activity. Problems can arise when animals exhibit inappropriate responses to humans. For example, failing to habituate to non-threatening human disturbance may compromise fitness, through increasing stress levels (Ellenberg et al., 2007, 2009) or leading animals to avoid disturbed habitats that are otherwise of suitable quality (an "undervalued resource"; Gilroy and Sutherland, 2007). In some cases, exhibiting the "correct" response during human-wildlife encounters can also be problematic. For instance, habituated animals may exploit anthropogenic food sources that are easy to obtain, but that compromise health (Waterman et al., 2019) or bring them into conflict with humans (Breck et al., 2019; Goumas et al., 2019). In the latter case, some individuals may present a greater cause for concern than others due to their reduced fear of humans ("problem" individuals; Swan et al., 2017). Likewise, the deleterious effects of human disturbance may disproportionately impact certain individuals, depending on factors such as temperament or reproductive state (Dyck and Baydack, 2004; Ellenberg et al., 2009). Knowledge of the proximate and ultimate mechanisms underlying variation in responses to human-wildlife encounters is therefore valuable in deciding whether specific individuals or groups need to be targeted for conservation or management interventions (Swan et al., 2017).

Cognitive research can provide an important tool in mitigating the impacts of human-wildlife interactions (Greggor et al., 2014, 2019; Barrett et al., 2019). Understanding how animals perceive and respond to humans can be used to limit impacts on wildlife populations by creating spatial or temporal "buffer zones" (Rodríguez-Prieto and Fernández-Juricic, 2005; Mallord et al., 2007; Gaynor et al., 2018); encouraging establishment in high-quality habitat (Gilroy and Sutherland, 2007; Greggor et al., 2019); or identifying the factors causing some species or individuals to exploit anthropogenic food sources (Swan et al., 2017; Barrett et al., 2019). A conceptual framework developed by Greggor et al. (2014) outlines how the problems caused by human-induced rapid environmental change can be mitigated by identifying the relevant perceptual and cognitive mechanisms underlying behavior. Applied in the context of direct encounters between humans and wildlife, key questions arise at the following levels: (i) perception – which human cues facilitate animal decision-making, and how are these cues perceived and categorized by the animal in question?; (ii) learning – how does experience influence decision-making, and what are the cognitive processes involved? Once the relevant cognitive and perceptual processes have been identified, they can be targeted to achieve (iii) the desired change in behavior (Greggor et al., 2014, 2019). Fundamental cognitive research has already been instrumental in helping to solve some conservation problems (e.g., O'Donnell et al., 2010; Urbanek et al., 2010); but few studies have applied this framework to manipulate behavioral responses to humans themselves, though some progress is being made. For example, recent experiments with urban herring gulls (Goumas et al., 2019, 2020) show that these birds use gaze and other human behavioral cues when selecting anthropogenic food, suggesting that simple changes in human behavior could help to reduce conflict between humans and herring gulls in urban areas.

FUTURE DIRECTIONS

In light of unprecedented rates of environmental change, further research into the responses of wild animals to encounters with people is urgently needed. Controlled experiments can be effectively used to elucidate the cognitive mechanisms underpinning wild animals' responses to humans, both across a range of habitats that vary in their frequency of human-wildlife encounters and where humans present varying levels of threat. Long-term field studies, where individuals can be accurately identified and monitored over time, are particularly valuable in this regard. Firstly, by experimentally manipulating the various aspects of human-wildlife encounters, we can identify relevant cues involved in risk assessment; how these cues are perceived and categorized; how previous experience shapes decision-making, and how information about people is transmitted through populations (Cornell et al., 2011; Sih et al., 2011). Secondly, by monitoring the behavioral responses of known individuals over time and across contexts, we can begin to determine how and why individuals differ in their responses to people. Response measures could be complemented with assays of personality and cognitive ability (Sih and Del Giudice, 2012; Dougherty and Guillette, 2018), in order to examine how these factors interact to influence decision-making. While the question of how cognition interacts with personality to determine behavior is attracting growing interest, relationships uncovered to date suggest a complex picture (Dougherty and Guillette, 2018). Field studies that generate robust measures of personality and cognitive ability from individually-identifiable animals, in a range of habitats and contexts, would therefore be extremely valuable.

Studies of animals living in human-dominated habitats must be complemented by studies of their rural counterparts, in order to determine the selection pressures acting on behavior. Although recent years have seen a proliferation of studies quantifying behavioral differences along urban-rural gradients, few studies identify the relevant mechanisms involved in generating this variation. Moreover, with the exception of studies examining the role of neophobia and categorization (Greggor et al., 2016), the cognitive processes underlying urban-rural differences in behavior have been largely overlooked. While the majority of evidence to date supports behavioral plasticity as the main driver of urban-rural differences in behavior, non-random sorting may be relevant in cases where dispersal propensity and tendency to colonize urban habitats covary with other behavioral traits. Natural selection may also be at work if behavior is heritable and contributes to individual fitness (Sol et al., 2013). Finally, by identifying the fitness consequences of individual variation in responses to human disturbance, we can also begin to investigate the broader ecological consequences. To this end, studying organisms with different life-history strategies (Maspons et al., 2019) and occupying a range of trophic levels would allow researchers to uncover how wild animals' responses to humans affect population dynamics, species distributions and community composition.

While the recommendations outlined above are ambitious, expanding research on the responses of wildlife to human encounters can play a pivotal role in reducing the impacts of human activity. Many long-term, individual-level behavioral studies already exist around the world, which are likely to provide suitable systems for investigating these types of questions. Studies covering a range of different species and habitats, where humans vary in the nature of their relationship with wildlife, provide an opportunity for "natural experiments" to identify how interactions with humans shape animal cognition and behavior. It would be particularly interesting to carry out these studies in areas experiencing relatively recent and/or rapid expansions of human activity. However, given that all habitats on Earth are now impacted by human activity to some degree (Ellis, 2011; Waters et al., 2016), it can often be difficult to obtain accurate information about wild animals' previous exposure to humans. To this end, simulation models supported by empirical evidence may be particularly useful in improving our understanding of the anthropogenic pressures facing wildlife around the world and their long-term consequences. Finally, we would encourage the publication of all studies, including null results and contradictory findings, in order to refine methodologies, quantify empirical support for existing theory and develop new theoretical frameworks, and improve the reliability of results (van Assen et al., 2014).

CONCLUSION

Living alongside humans is a challenge for many wild animals, particularly in scenarios where people differ in their behavior toward wildlife. How wild animals respond during encounters with humans is likely to be controlled by a range of cognitive processes, and may carry important fitness consequences. In this review, we have considered the role of animal cognition in human-wildlife encounters, and its important influence on the ability of individuals, populations and species to cope with life in a human-dominated world. Further research in this area is vital to identifying the selection pressures on animal cognition associated with human-induced ecological change, and would assist in mitigating the negative impacts of human activity.

AUTHOR CONTRIBUTIONS

MG and VL co-wrote the manuscript with guidance and significant input from NB, LK, and AT. All authors contributed to the article and approved the submitted version.

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GLOSSARY

Appetitive behavior/stimulus	Characterized by attraction as a result of an animal's requirement to meet bodily needs
Associative learning	Learning that results from experiencing contingencies, or predictive relationships, between events (Shettleworth, 2010)
Aversive behavior/stimulus	Characterized by repulsion as a result of an animal's requirement to avoid harm
Behavioral plasticity	The ability of animals to formulate behavioral responses to cope with new or unusual challenges (Ducatez et al., 2020)
Categorization	An organism's ability to respond equivalently to members of the same class, to respond differently to members of different classes, and transfer those responses to novel, discriminably different members of these classes (Lazareva and Wasserman, 2010)
Class-level recognition	(i) Receivers learn the signaller's individually distinctive characteristics and associate these characteristics with inferred class-specific information about the signaller; and (ii) receivers match the signaller's phenotype to an internal template associated with different classes (Tibbetts and Dale, 2007)
Discrimination	The act or process of distinguishing between stimuli or of recognizing or understanding the differences between things (Colman, 2008)
Generalization	The tendency for a learned response to a particular stimulus to be elicited by other stimuli that resemble it (Colman, 2008)
Habituation	A form of non-associative learning involving decreased responsiveness to a stimulus with repeated presentation (Blumstein, 2016)
Individual recognition	A subset of recognition that occurs when one organism identifies another according to its individually distinctive characteristics (Tibbetts and Dale, 2007)
Observational conditioning	Associating a cue or object with an affective state or behavior(s) by virtue of watching demonstrators respond to it (Shettleworth, 2010)
sensitization	A form of non-associative learning involving increased responsiveness to a stimulus with repeated presentation (Blumstein, 2016)
Social learning	Learning that is influenced by observation of, or interaction with, another individual or its products (Heyes, 1994)

frontiers in Veterinary Science

REVIEW
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The Power of a Positive Human–Animal Relationship for Animal Welfare

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Domestic animals often seek and enjoy interacting with humans. Positive human–animal relationships can elicit positive emotions and other positive welfare outcomes. Nevertheless, our understanding of the underlying processes that govern the positive perception of humans by animals is incomplete. We cover the potential mechanisms involved in the development and maintenance of positive human–animal relationships from the perspective of the animal. This encompasses habituation, associative learning, and possibly attachment or bonding based on communication and social cognition. We review the indicators from the literature to assess a positive human–animal relationship. We operationally define this positive relationship as the animal showing voluntary approach and spatial proximity (seeking) and signs of anticipation, pleasure, relaxation, or other indicators of a rewarding experience from interacting with the human. For research, we recommend accounting for the baseline human–animal relationship in the animal's everyday life, and incorporating a control treatment rather than only comparing positive to negative interaction treatments. Furthermore, animal characteristics, such as previous experience, genetics, and individual predisposition, as well as contextual characteristics related to the social and physical environment, may modulate the perception of humans by animals. The human–animal relationship is also influenced by human characteristics, such as the person's familiarity to the animal, attitudes, skills, and knowledge. We highlight implications for current practices and suggest simple solutions, such as paying attention to the animal's behavioral response to humans and providing choice and control to the animal in terms of when and how to interact with humans. Practical applications to achieve a positive perception of humans could be better utilized, such as by incorporating training principles, while keeping in mind trust and safety of both partners. Overall, there is growing evidence in the scientific literature that a positive human–animal relationship can bring intrinsic rewards to the animals and thereby benefit animal welfare. Further research is needed on the underlying processes to establish an effective positive human–animal relationship, especially in regard to the type, frequency, and length of human interaction necessary. In particular, the importance of providing animals with a sense of agency over their interactions with humans remains poorly understood.

Keywords: agency, domestic, interaction, inter-species, perception, positive welfare, welfare assessment, well-being

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INTRODUCTION

The human–animal relationship (HAR) is an important determinant of animal welfare (1–3). Numerous studies have demonstrated the detrimental effects of a negative HAR on animal and human welfare, that is, productivity, companionship, health (4). A negative HAR can impair animal welfare with negative consequences on the animal's productivity, health, and welfare, primarily through fear as an underlying mechanism (1, 5). In comparison, the benefits of a positive HAR for animal welfare are poorly understood and appreciated. Domestic animals often seek and enjoy interacting with humans, beyond depending on humans for food (6–9). Animals may perceive interacting with humans *per se* as rewarding (5, 10, 11).

This review compiles the recent knowledge of the welfare benefits for animals of interacting positively with humans and provides recommendations to assess and utilize a positive HAR. We focus on the HAR from the perspective of the non-human animal (hereby referred to as "animal") unless stated otherwise. For the HAR from the human's perspective, we refer the readers to other reviews (5, 12, 13). We restrict the scope of this article to domesticated species, primarily farm and companion animals, because they have been (and still are) selected over thousands of years with a major influence on their response to humans (9, 14), and most domestic animals experience frequent interactions with humans. Notwithstanding, animals from other species are also able to develop positive relationships with humans, for instance, animals kept in zoos (1, 15, 16) or laboratories (17, 18), and therefore examples on these species are included where relevant.

MECHANISMS FOR THE FORMATION OF A POSITIVE HAR

Definitions

A positive HAR can be defined conceptually based on a positive perception by the animal of the human. Because perception is challenging to assess practically, a positive HAR can be defined operationally in that the animal shows voluntary approach and spatial proximity (seeking) and signs of anticipation, pleasure, relaxation, or other indicators of a rewarding experience arising from interacting with the human. Fear of humans prevents a positive perception of humans, but low or no fear is in itself not a sufficient condition. A positive HAR brings beneficial short-term [e.g., positive emotions (19)] and long-term [e.g., stress resilience (20)] welfare outcomes for the animal when or after interacting with the human (see section Implications for Practice).

Habituation

HARs are most often referred to in the context of fear of humans (21), although positive HARs have received increased attention recently (1–3, 22, 23). This questions whether a positive HAR can be understood, as for negative HAR, solely as a consequence of a reduction in the fear response to humans or an absence of fear. When a stimulus is unfamiliar, fear is usually the default response. Fear of humans can be reduced through habituation, defined as a reduction in response resulting from repeated exposure to a stimulus (24). Although it can reduce fear of humans by leading to a neutral response, habituation is insufficient to reach a positive HAR. This non-associative learning process can occur by direct exposure, but also be facilitated or inhibited by social learning or transmission from the dam or other animals (25, 26).

Interactions vs. Relationship

The formation of a relationship is a progressive process, reinforced upon subsequent interactions. This highlights the difference between an interaction and a relationship based on a single vs. multiple events between two individuals, respectively (27), with a relationship developing on the basis that animals are able to memorize and predict future interactions with humans (28, 29). We focus on the relationship rather than interactions because the HAR is more relevant for welfare because of its long-lasting and integrative nature (i.e., comprising past interactions, present, and predicting future ones). Of course, there is a link between interactions and the resulting relationship. In particular, the formation of a positive HAR may be jeopardized by negative interactions, even when the occurrence of positive interactions far outweighs negative interactions (30). However, a strong or high-quality HAR may endure deviation from positive interactions or be more resilient to aversive events (31, 32). The time at which a relationship is formed remains difficult to determine, but it can be defined as the time at which the animal forms expectations of its interaction with humans.

Associative Learning

Associative learning can accelerate the formation of a relationship, by the animal associating humans with positive aspects either through classical conditioning (the human presence itself or its concurrent association with a positive event) or operant conditioning (interacting with the human leads to positive consequences). A positive HAR can be established by human contact that is inherently rewarding such as through stroking or brushing [dog (33), sheep (6, 7), cattle (11, 34, 35), pig (36, 37)] or play interactions [dog (38), cat (39)]. However, not all individuals react in the same manner to putative positive interactions. For example, previous interactions affect the way animals perceived human contact [pig (32, 40)], supporting a role for ontogeny. Furthermore, animals from different genetic origins can also perceive stroking by humans differently [dog (9), sheep (41)], supporting a role for phylogeny. The role of potential modulating factors such as individual differences (e.g., personality) and affective states should be investigated further. It should be noted that a positive HAR cannot simply be explained by food or other resources provided by humans, although food can facilitate the development of a positive HAR [sheep (7), cow (42), pig (8), cat (39)].

Bonding

In addition to associative learning processes, a number of phenomena have been proposed to explain the formation of a positive HAR, in particular aspects relevant to social bonding and related constructs. Familiarity with a human does not necessarily equate to a positive HAR, although it may be conducive to it given that repeated non-aversive exposure can facilitate positive appraisal ["the mere exposure" effect (43)]. The attachment theory has been used in the context of the HAR (26), originating from the study of infant–parent relationships and defined as an affectional bond binding the individuals together in space and enduring over time (44). Without any obvious reinforcement, and because animals need to feel safe and have a basis from which they can explore their world, attachment can occur with familiar individuals such as the mother, peers, other conspecifics, and even individuals from other species such as humans (26). These animals calm quickly after a short period of social isolation when in the presence of a familiar human [dog (33, 45), cat (46), hand-reared lamb (26, 47), pig (48)]. The socialization process (49, 50) may also play a role in the context of the HAR, through learning how to behave toward others. Indeed, a successful relationship encompasses both the intent by the animal and the human to interact, as well as competent social skills relying on sociocognitive and communicative abilities (see other contributions in this Special Issue).

ASSESSMENT OF A POSITIVE HUMAN-ANIMAL RELATIONSHIP

The HAR can be observed either through observations of spontaneous interactions (i.e., without interference) or through stimulus-evoked situations and tests that investigate the HAR in a more systematic way.

Indicators

A number of biological changes can occur before, during, and/or after interactions with humans (**Table 1**). Most of these indicators are based on features of the interactions, indirectly reflecting the HAR. Some indicators can distinguish different qualities of the relationship (e.g., evaluate which animals have a better relationship than others), but it is generally difficult to set a threshold where a positive HAR starts, apart from some indicators that clearly reflect a positive HAR. The assessment of a positive HAR requires a holistic analysis, given that several indicators need to be considered together for a full understanding. Care is required in assessing a positive HAR because, for example, the motivation to interact with humans may at the time be conflicting with other motivations, and some indicators of a positive HAR are species-specific.

Behavioral Changes

We describe here in a typical chronological order the behavioral changes associated with a positive HAR and their specificity to a positive HAR.

The animal can show signs of anticipation before the interaction takes place in cases when the human interaction is predictable or environmental cues signal the arrival of a human. These could be considered "appetitive" signs, such as pacing, vocalizations, or increased behavioral transitions (83). For example, captive Bottlenose dolphins anticipated interactions with humans, through increased surface looking and spy hopping, and these anticipatory behaviors correlated with their subsequent level of engagement in the interaction (84). These anticipatory signals can nevertheless be ambiguous indicators, as either indicative of positive (excitement) or negative (frustration, for instance, if the delay is too long) states depending on the situation (83).

The first reaction of an animal to the arrival of a human in its environment is an orientation response. The animal typically turns its attention toward the human, possibly using various senses other than vision. The orientation response indicates that the animal notices the presence of the human but is not in itself an indicator of the quality of the HAR because of its potential ambiguous underlying motivations reflecting either a positive (e.g., interest) or negative (e.g., vigilance) state. However, head, ear, and body posture or movement and accompanying behaviors may help to distinguish at least between a negative HAR and a neutral to positive HAR; for example, in cattle, head stays in normal position and ears not erected or even hanging loosely while looking toward the person and ongoing rumination.

Once the human enters the animal's environment, the latency to approach, in the form of voluntary seeking behavior of the animal, is generally an indicator of a positive HAR and/or curiosity. Approach is context-specific (e.g., novelty of the situation and stimulus) and species-specific and therefore should be used with other indicators. However, a lack of approach does not preclude a positive HAR but may just indicate low motivation for (physical) interaction at this time (68); this especially accounts for situations in the home environment where many distractions or competing motivations may occur (e.g., feeding, resting). In many cases, spatial proximity is also a sensitive indicator of a positive HAR, for instance, reflected by the duration of time spent near a human (30, 51).

The number or duration of interactions initiated by the animal is often used as an indicator of the quality of the HAR. Although a quantifiable metric, it does not necessarily reflect the relationship because the animal may modulate the interaction with the human according to its needs; for instance, the animal may want to interact more if it is distressed, may not have interacted for some time, or conversely may not be interested at that time in interacting (68). In this regard, further research is required on refined indicators of interactions (85), such as by studying the complementarity, reciprocity, and synchrony of behavioral exchanges that have been shown to be important in the quality of parent–infant interactions (70). For instance, behavioral synchrony has been shown to be linked to affiliation in humans (86), and locomotor synchrony has been observed between dogs and their owners (69). Further, dogs with lower initial oxytocin levels received more stroking from their owner (87), demonstrating the dynamic interplay of the HAR.

The type of behaviors and body posture displayed during approach and contact with humans, reflecting the animal's level of engagement in the interaction, can provide information regarding the perception and motivation of the animal. In particular, solicitation behaviors such as species-specific grooming solicitation postures and other types of physical solicitation for contact such as touching, nudging, scratching the human with the paw, or vocalizations are indicators of the animal's motivation to engage and can be interpreted as clear signs of a positive perception of the human. Animals may also expose body areas where they wish to be stroked, for example,

TABLE 1 | List of indicators of a positive human–animal relationship.

Category	Indicator	Examples of measures	Direction of change	Specificity[1]	Key references
Movement/location	Approach[2]	Latency to approach/touch human	⇩	Conditional	(22)
		Direction of movement relative to human	⇔	Conditional	(22)
	Spatial proximity	Time in proximity of human	⇧	Conditional	(30, 51)
Expressive behaviors	Vocalizations[2]	Yapping, purring, chirping, grunting, other low-frequency vocalizations	⇧	Conditional	(46, 48)
	Ear posture[2]	Relaxed ears	⇧	Yes	(52–58)
	Tail posture	Tail low, or wagging	⇧	Conditional	(59)
	Body posture	Relaxed, laying down near the human	⇧	Yes	(48)
	Facial expression	Muscle movement, change in facial display, closed/half-closed eyes	?	?	(60, 61)
Qualitative behavior assessment		Positively valenced factors	⇧	Yes	(62)
Preference for human[2]		Choice or motivation for specific human(s) over other stimuli, memory of humans	⇧	Conditional	(28, 32, 36, 48, 63, 64)
Characteristics of the interaction	Initiating physical interaction[2]	Exposing a body area	⇧	Conditional	(35, 37, 52, 65)
		Solicitation behaviors like nudging, scratching, play bow	⇧	Yes	(66)
	Interaction features	Frequency or duration of physical contact, eye gaze	⇧	Conditional	(67)
	Reaction to human contact	Acceptance of stroking or touch	⇧	Conditional	(68)
	Behavioral synchrony	Temporal synchrony of behavioral exchanges/movement	⇧	?	(69)
	Behavioral matching	Complementarity, reciprocity of behavioral exchanges	⇧	?	(70)
During or postinteraction effects	Relaxation[2]	Duration or shorter latency to rest or sleep, rumination	⇧	Yes	(55, 71–74)
	Exploration[2]	Secure base exploration	⇧	Conditional	(26, 50)
Postinteraction behavioral changes	Separation distress[2]	Searching behavior, distress vocalizations, or contact calls	⇧	Conditional	(47, 51, 75, 76)
Physiological indicators	Oxytocin[2]	Hormone concentration or change	⇧	Conditional	(77)
	Heart rate[2]	Heart rate beat per min	⇩	Conditional	(54, 78, 79)
	Parasympathetic activity[2]	Heart rate variability: high-frequency band, RMSSD	⇧	Conditional	(54, 78, 79)
Cognitive and neurobiological measures	Cognitive bias	Positive judgment of ambiguous cues	⇧	Conditional	(40, 80)
	Neurobiology	EEG, fNRIS, neuroimaging (e.g., MRI, PET scan), postmortem measures	⇧ or ⇩	Conditional	(37, 81, 82)

These are general indicators, and their expression may be species-specific. This table aims to stimulate discussion and consideration of the complexity of positive HAR assessment and our current state of knowledge on its assessment.

[1] *"Conditional": the presence of this sign could indicate a positive HAR, but may need to be interpreted in conjunction with other indicators or the context (e.g., conflicting motivations).*

[2] *The presence of this sign could indicate a positive HAR, but its absence does not necessarily rule out a positive HAR.*

the ventral neck area in cattle (35, 52), the abdominal area in pigs (37), or the back rather than the head region in dogs (65). These types of behavioral responses, exposing often vulnerable body region, may be interpreted as involving a level of trust reflecting a positive HAR, although some behaviors such as lying with the belly exposed may also indicate submission in dogs, for instance, and therefore do not necessarily indicate a positive HAR. In most cases, these behaviors are similar to those shown during intraspecific sociopositive interactions, although there are some interspecies specific behaviors [e.g., dog vs. wolf (88)].

The response of the animal in the presence of the human is obviously a key indicator of a positive HAR. A lack of avoidance response to humans is usually indicative of low fear of humans (22). Ear position changes or positions (forward vs. side or backward, or erected vs. hanging) have been used to interpret the valence of human contact [sheep (53, 54), cow (52, 55, 56), dog (57), horse (58)], and recent work investigated more subtle changes in facial expression [cat (60), parrot (61)]. Tail wagging in dogs is often cited as an indicator of enjoyment, but it may be a sign of arousal rather than specifically positive valence (59). In some species, some vocalizations are often associated with positive interactions, for instance, purring in cats (46). A rapid reduction in distress vocalizations and increased proximity seeking toward humans can also be interpreted as a positive perception of human presence [goat (75, 76), hand-reared sheep (47, 51)]. Redirected or displacement behaviors [e.g., in dogs yawning, lip- or muzzle-licking, and looking away or toward the ceiling (89)] may be negative indicators, reflecting a reluctance to interact or conflicting motivations. Similarly, pigs that were used to stroking or scratching expressed more high-pitched vocalizations when the handler did not provide gentle tactile contact, which the authors interpreted as indicators of stress possibly resulting from frustration due to the fact that the previously-handled piglets expected positive human contact (90).

Finally, qualitative behavior assessment in which human observers rank the bodily expression of the animals using word descriptors (91) seems promising as a holistic approach for differentiating HAR (62).

Behavioral changes to assess a positive HAR may be species-, individual-, and context-specific (see section Implications for Practice). In particular, the way the human and the animal initiate the contact or interact appear as important modulators of these changes [pig (92), dog (65, 66, 78, 87)].

Physiological Changes

In addition to behavioral changes, studies have also shown a wide array of physiological changes linked to human–animal interactions (93).

Oxytocin, in particular, has attracted a lot of attention for its link to social processes. Positive interactions, in particular with familiar humans, generally raise oxytocin concentration [reviewed in (77)]. The relationship between positive HAR and changes in oxytocin concentrations is nevertheless complex and not fully understood [dog (66, 67, 79, 87); sheep (94); domestic species (77); dairy cattle, pig, goat (95)].

Cortisol concentration also changes following positive interactions, with the direction of change reflecting either excitement [dog (79)] or conversely relaxation [dog (66)], and change in cortisol concentration is time- and context-dependent.

Heart rate and heart rate variability measures provide dynamic information on activation of the autonomic response. In general, studies show a reduced heart rate and an increase in measures of parasympathetic activation (e.g., high frequency, or greater root mean square of successive differences) during or after interacting positively with a human [sheep (54); dog (78, 79)], partly dependent on the body region of grooming [horse (96); cow (52)] or the type of interactions (97).

Finally, the involvement of other physiological changes, especially neurotransmitters such as opioids and dopamine and immune parameters, such as immunoglobulin-A require further research. In fact, positive interactions induce an array of physiological and immune changes in both humans and animals (93), and -omics approaches [e.g., transcriptomics, proteomics, metabolomics (98)] could be useful to decipher the biological pathways modulated by positive HAR and its effects on health. For instance, rabbits that received regular positive human contact showed lower incidence of atherosclerosis (99). Gently handled chickens had a higher immune response and disease resistance (100), and mere regular visual contact with humans increased the antibody response to Newcastle disease vaccine and reduced heterophil-to-lymphocyte ratio following capture and restraint later in life (101).

Cognitive and Neurobiological Effects

Few studies have focused on the cognitive and neurobiological changes induced by a positive HAR. Cognitive bias tasks have recently been popular as an indirect assessment of emotional states by studying affect-related cognitive changes (102). In rats, tickling by a human induces a more positive judgment of ambiguous cues, suggesting that it induces a positive emotional state (80). Similarly, piglets that experienced positive human contact judged ambiguous cues more positively (40). Conversely, dogs show a more negative judgment of ambiguous cues after being left alone (103). Whether a positive HAR leads to positive emotional states requires further research.

Other approaches have relied on the animal's memory of humans. Pigs can remember positive interactions with humans for at least 5 weeks (32). Horses that were trained using positive reinforcement training with positive human interactions remembered the human 6 months later and spent more time close to the familiar human (63). Sheep can be trained to discriminate sheep and human faces (104) and remember those faces for over 2 years (28), and sheep also recognize their familiar caretaker without any pretraining (64). These findings support that a positive HAR can be long-lasting.

Finally, neurobiological studies of positive HAR are still in the early stage with the use of, for instance, functional near-infrared spectroscopy [dog (81)], electroencephalography [pig (37)], or postmortem brain measures [sheep (82)]. Our understanding of the neuroscience of human–animal interactions could progress with new techniques such as neuroimaging [dog (105)], allowing non-invasive longitudinal neurobiological studies.

Postinteraction Changes

Most studies have focused on studying those biological changes when or around the time a human is present. There are also a number of changes that can occur following positive human–animal interactions, that is, at other times than when the animal and human interact. These can be indicative of positive (relaxation or "postconsummatory") or negative (e.g., separation distress, searching behavior) effects. These effects that outlast the interaction *per se* are often overlooked as compared to the changes occurring during the interaction. Indices of relaxation include hanging ear posture [cattle (55)], lower heart rate [dog (71)], greater parasympathetic activity [various species (72)], elevated brain oxytocin concentration [pig (73)], and shorter latency to rest or better sleep quality [dog (74)].

There can also be indicators of attempts to restore contact, for example, after interruption of an interaction, as evidenced by signs of separation distress or searching behavior [dog (45); hand-reared sheep (47)]. Although these may be signs of distress and negative emotional states, searching behavior and separation distress when an interaction is disrupted are nevertheless signs of a positive HAR.

Further research is warranted on whether a positive HAR can induce baseline biological changes on an animal, for example, changes to its time-budget outside of the interactive sessions with humans. For instance, gentle human interactions during milking or rearing can lead to fewer aggressive interactions between dairy cows once they return to the herd (106) and lower adrenocortical activity in calves (107). Similarly, flocks of gently handled chickens showed fewer agonistic interactions (108).

Epistemiological Considerations for the Investigation of a Positive Human–Animal Relationship

Motivation and preference tests can be used to assess the HAR (22). They can provide insight into the animal's perception (109), by testing animals on what they find positively and negatively reinforcing; what they want or do not want and how much they value the stimulus. Nevertheless, preferences and motivation may vary with the time of day, environmental conditions, the animal's previous experience, and the current condition and familiarity with the options under study (110), requiring careful interpretation.

The most common tests used for HAR assessment have been the stationary/passive human test, approaching/active human test, and tests involving separation from a human [reviewed in (22)]. We cover below various aspects of the development and use of tests to specifically assess a positive HAR.

An animal voluntarily approaching and interacting (non-aggressively) with a human is a prime indicator of a positive HAR. This is nonetheless not sufficient to qualify as a specific positive HAR indicator because the animal may approach and interact because of curiosity or a motivation to explore. The motivation to explore may also be initially affected by how fear-provoking the situation is. Conversely, the lack of approach is not sufficiently conclusive to reject a positive HAR due to potentially conflicting motivations and a momentary lack of motivation for interaction.

Tests based on avoidance responses (e.g., distance of withdrawal by the animal from an approaching human) are often used to measure the fear dimension of the HAR. However, acceptance of approach and subsequent touch and stroking by a human are clear indicators of a positive HAR and can be more sensitive in differentiating the quality of HAR than approach behavior toward a stationary person [pig (36, 92), cattle (35, 68, 111)]. The sensitivity of the tests nevertheless depends on the species tested and contextual features (22), as well as phenomena such as generalization of the response toward unfamiliar humans.

Situations where there is a lack of control offered to the animal because the animal is restrained or limited to a constrained space or when contact is imposed on the animal without the possibility for the animal to avoid or withdraw may influence the validity of the HAR assessment. Nevertheless, the few studies to date comparing restrained and unrestrained animals showed relatively similar responses to humans (68, 112, 113). Standardized interactions by the humans, such as imposing contact on the animal or using highly standardized interactive features (e.g., predetermined interaction in terms of bout frequency or duration) are commonly used in research settings as they provide experimental control. However, free-choice interactions may replicate real-life situations more faithfully because control over the situation may be linked to the perception of the situation, although this hypothesis remains to be tested. It may be important that the animal is provided with a sense of control or agency (114) by free-choice approach about when and how to interact (61, 78). This is similar to the case for second-person neuroscience (85) that emphasizes the need to look at situations of active social engagement and reciprocal behaviors, rather than passive observation or being subjected to a situation with a lack of agency. This argument is based on the fact that an interaction typically involves active participation from both agents.

The test should be conducted in an appropriate environment. Animals have been most often tested individually, which may not reflect their typical reaction when in their social group. Furthermore, testing environments have most often been barren, offering few choices other than interacting with the human. Hence, this questions the specificity and validity of the animal's response toward the human as an indicator of a positive HAR in cases where there is a lack of choice (110).

The experience of the animal with humans is obviously crucial to consider, as additional positive interaction treatments may fail to show additional effects if the HAR is already positive (107, 115). Hence, it is important to assess the "baseline" HAR in the animal's real-life environment (i.e., outside of the experimental treatments) and take into account the ratio of negative and positive human contact (106).

Many studies, to date, compared positive and negative human interaction treatments, but lacked a control treatment [e.g., (73, 74, 116)]. This control treatment usually consists of minimal human contact involved in routine care and management (117), or human present with no active interactions (52). It is crucial to demonstrate that the HAR is specifically positive, rather than neutral. If comparing only positive and negative interactions without a control treatment, a potential difference may be induced by negative treatment effects without being able to distinguish them from the positive treatment effects.

As mentioned earlier, more detailed analysis of the interaction could assist in assessing the quality of the HAR, for instance, based on the synchrony between partners (69), or the functional complementarity of the exchange and/or responsiveness using similar approaches to those used in humans (70).

IMPLICATIONS FOR PRACTICE

Developing and Cultivating a Positive Human–Animal Relationship: How?

The HAR is a dynamic and reciprocal process modulated by individual and contextual features. An understanding of its development and regulatory mechanisms provides practical opportunities to develop and maintain a positive HAR for animal caretakers.

Gentle handling is particularly effective [sheep (6), pig (32, 92), ostrich (118)], although passive human presence may be required initially to habituate the animal [pig (36)]. Note that some species may not need physical contact, and visual contact may be sufficient [e.g., poultry (119, 120)], although the need for and type of contact are strongly species-dependent. Positive interactions involve several species-specific sensory channels: tactile, visual, auditory, and olfactory, and are often multimodal [dairy cow (121), sheep (82), pig (23)]. In many species, brief (from 15 s to a few minutes) opportunities to interact with humans over days or several weeks are sufficient to reduce the animal's fear of humans and encourage approach and interaction [dog (33), horse (122), cattle (123), pig (92, 124), poultry (120)], suggesting that a positive HAR from the perspective of the animal can develop rapidly. Studies examining tickling of rats on positive affective states have demonstrated the importance of the dosage and characteristics of this technique (125). Further research is needed to determine the minimal "dose" of human contact required to form a positive HAR in terms of type, frequency, and duration of interaction.

Incorporating training principles, primarily through the use of positive reinforcement, has been broadly and successfully used in practice for zoo and companion animals to improve handling by reducing the aversiveness of some procedures [dog (126), cat (127), horse (63), primates (128)]. Training is not yet commonly used in farm settings despite proof of its effectiveness in research settings [pig (129, 130), sheep (131), cattle]. Given that human contact *per se* can be perceived as inherently rewarding, it could be used as a reward during training (e.g., stroking, brushing, playing), although food rewards may facilitate this process.

It may be easier to develop a HAR with young animals [dog (132), pig (124)] because they may had fewer negative experiences with humans, have greater learning ability (133) and higher levels of curiosity and exploration (26, 50) than adult animals. In particular, the development of a HAR may be most effective during sensitive periods for socialization such as during early life (49) or socially stressful periods such as after weaning (134). Social facilitation, building on the transmission of the HAR with the dam or other conspecifics, can also be effective [horse (135), sheep (26), pig (136)]. There is even evidence of transgenerational transmission of positive HAR, as human contact altered mother quails' egg physiological environment and led to less emotionally reactive offspring (137).

Familiarity and previous experience with humans can influence the HAR. Nevertheless, if the animal's experience with familiar humans is mainly positive, domestic animals can generalize their positive response toward unfamiliar humans [sheep (138–140), dog (141, 142), pig (8, 10, 36), horse (143), cattle (34)], although the animal may still prefer familiar over unfamiliar humans [sheep (116)]. Generalization of the HAR to unfamiliar humans depends not only on past experiences but also familiarity of the context such as the behavior or other characteristics of the human and the location [cattle (42, 144, 145), pig (32, 36, 90, 146)], which may affect the motivation to approach and remain near an unfamiliar human. As such, a positive HAR is not necessarily limited to a personalized one, that is, toward a specific human.

It is important to keep in mind the potential modulating effects on the HAR due to genetics and species differences [fox (147), dog (9), sheep (41)], individual differences [dog (78)], previous experience and age [pig (32, 36)], social context [cattle (148), sheep (26), pig (136)], and other context-specific aspects.

In addition, the attitudes, skills, and knowledge of humans influence their behavior toward animals and in turn the animal's perception of humans (1, 5). Although beyond the scope of this article, these human factors should be considered when thinking of the HAR. There is also increasing evidence that animals can recognize human facial expression of emotions [dog (149–151), horse (152), goat (153)] or human bodily expression [cat (154)] and prefer positive human emotional expressions.

The predictability of the interaction can strongly affect the animal's response to humans [pig (30), beef cattle (144), sheep (116), dog (155)], because as mentioned previously the relationship is based on the animal's expectation of its interaction with humans. The HAR concept implies the predictability of human–animal interactions. In addition, the provision of choice and control available to the animal in terms of when and how to interact appears to be important [dog (79), pig (92), cattle (11)].

A key aspect for the human is to pay attention to the animal's response to humans. A positive HAR can be assessed based on behavioral observations as highlighted previously (see section Assessment of a Positive Human–Animal Relationship), and as such it is feasible to cultivate a positive HAR in practice based on this knowledge and without the need for specific equipment.

The Benefits of a Positive HAR: Why?

The HAR can have important and long-lasting effects on the welfare of animals, and this relationship is often critical to the domestic animals' role, for example, animal productivity and ease of handling and management, as well as companionship and satisfaction for the human. Evidence is accumulating on the potential welfare benefits of a positive HAR (**Figure 1**).

There are benefits of a positive HAR on stress resilience. For example, offering positive interactions to shelter dogs can reduce their cortisol level (156) and combined with training increases adoptability (157). Walking and stroking shelter dogs for 15 min once a week for 6 weeks increased the time they spent visible from the front of the pen and tail wagging (158). Only three 10-min bouts of handling was sufficient for shelter dogs to show a preference for the handler (33). Five minutes of weekly brushing dairy heifers facilitated their acclimation to the milking routine (123). Five seconds of back scratching of sows for 1 week prior to farrowing reduced piglet mortality in sows (159), although this stroking treatment was confounded with music from a radio. These examples indicate that brief positive interactions with humans can benefit animal management and animal welfare.

A positive HAR can also buffer aversive procedures where humans are involved such as veterinary inspections or management interventions [sheep (131), pig (129), cow (160), ostrich (118)], presumably by removing human-related stress-eliciting components. In addition, humans can provide social support to animals during stressful times, especially for animals kept in suboptimal social environment [pig (161), sheep (47), chimpanzee (17)]. Stroking by the owner calms the behavioral and heart rate responses of dogs to subsequent separation (71). The effectiveness of providing social support can be modulated by the quality of the HAR [dog (66, 162)].

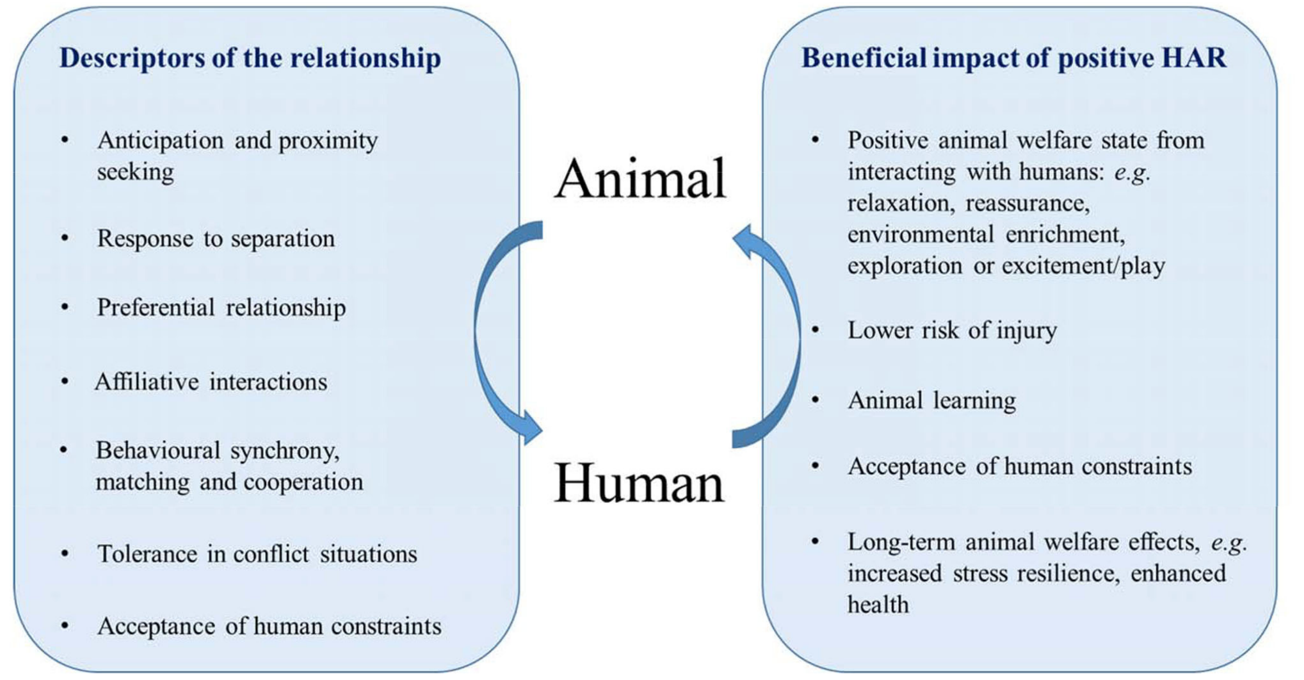

FIGURE 1 | The different dimensions of a positive human–animal relationship for the animal. The arrows symbolize the interactions between the animal and the human.

As an enrichment strategy, positive interactions with humans present several advantages as they usually occur daily and can be combined with routine checks, can be manipulated for their predictability to minimize habituation, and do not require additional resources (e.g., material). For example, orangutans preferred to stay in the part of their zoo enclosure where they can be close to and observe visitors (163), suggesting that interactions with humans may be enriching for them.

There is limited direct evidence to date that a positive HAR stimulates positive affective states in domestic animals (19). Tickling of rats (80) or gentle contact of pigs (40) by humans induces more positive judgment of ambiguous cues, suggestive of a positive emotional state. Positive or negative human interactions influence the sleeping patterns of dogs (74), although in the absence of a control treatment it remains to be determined whether this was the result of the positive or negative interactions.

Developing a positive HAR provides benefits in the long term. The persistence of the effect of early positive human contacts [5–16 weeks, pig (32, 124); 6 months, dairy cattle (11); 6–8 months, beef cattle (134); 24 months (164); 8 months, goat (76); 25 months, (165); 6–8 months, horse (63)] makes it an intervention with potentially long-lasting effects. Nevertheless, there may also be risks or disadvantages of a positive HAR. For example, pigs that experienced positive human interactions can be difficult to handle in familiar locations because of low fear of humans (166); however, pigs that are fearful of both humans and the unfamiliar handling location take longer to move and balk more than pigs that have experienced positive human interactions (146), suggesting an interplay between the HAR and the familiarity of the environment. It is also important to keep in mind trust and safety of both partners, because animals with low fear of humans can be dangerous, especially in case of inappropriate human behavior as it is often the case in dog bites of children (155) or during risky or potentially aversive procedures that involve close contact or handling [horse (25), dairy cow (121, 167)]. In order to be able to both manage the animals in a practicable manner and minimize the risks of aggression or injuries, a positive HAR may benefit from settings boundaries such as respecting a safe distance and avoiding potentially dangerous interactions. Social animals usually learn to distinguish acceptable from unacceptable social behaviors during their development as part of the socialization process and the development of their social skills, and this socialization process may also affect the animal's behavior toward humans.

Hence, a positive HAR can provide animals with positive welfare outcomes (20, 168), such as greater stress resilience, social support, environmental enrichment, possibly positive affective states, as well as benefits to their role for humans.

CONCLUSIONS

Positive experiences with humans lead to domestic animals seeking and interacting with humans. Consequently, a positive HAR can bring intrinsic rewards to the animal. It can be used to elicit positive emotions and other positive welfare outcomes. Nevertheless, our understanding of the underlying processes that govern the positive perception of humans by animals is incomplete and will benefit from further research, especially in regard to the type, frequency, and length of human interaction necessary to establish an effective positive HAR. In particular, the importance of providing animals with a sense of agency and its effect on the HAR remains poorly understood. Further research is needed to identify how much changes in features of interaction reflect the quality of the relationship.

AUTHOR CONTRIBUTIONS

J-LR wrote the first draft of the manuscript and drafted **Table 1**. XB drafted **Figure 1**. SW, XB, and PH edited the manuscript. All authors reviewed and approved the0 final manuscript.

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Gaze Following in Ungulates: Domesticated and Non-domesticated Species Follow the Gaze of Both Humans and Conspecifics in an Experimental Context

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Gaze following is the ability to use others' gaze to obtain information about the environment (e.g., food location, predators, and social interactions). As such, it may be highly adaptive in a variety of socio-ecological contexts, and thus be widespread across animal taxa. To date, gaze following has been mostly studied in primates, and partially in birds, but little is known on the gaze following abilities of other taxa and, especially, on the evolutionary pressures that led to their emergence. In this study, we used an experimental approach to test gaze following skills in a still understudied taxon, ungulates. Across four species (i.e., domestic goats and lamas, and non-domestic guanacos and mouflons), we assessed the individual ability to spontaneously follow the gaze of both conspecifics and human experimenters in different conditions. In line with our predictions, species followed the model's gaze both with human and conspecific models, but more likely with the latter. Except for guanacos, all species showed gaze following significantly more in the experimental conditions (than in the control ones). Despite the relative low number of study subjects, our study provides the first experimental evidence of gaze following skills in non-domesticated ungulates, and contributes to understanding how gaze following skills are distributed in another taxon—an essential endeavor to identify the evolutionary pressures leading to the emergence of gaze following skills across taxa.

Keywords: domestication, gaze following, social cognition, ungulates, human relation to animals

INTRODUCTION

Gaze following is the ability of looking where others are looking (Butterworth and Jarrett, 1991; Emery et al., 1997). This ability is often considered one of the most basic forms of social cognition, as it allows individuals to socially acquire relevant information about the environment (e.g., about food location, presence of predators, occurrence of social interactions among group members) (Tomasello et al., 1998, 2001) and also about others' interests and goals (Baron-Cohen, 1995). Therefore, gaze following might be highly adaptive for humans and other animals (Brooks and Meltzoff, 2002).

To date, gaze following has indeed been reported in a variety of taxa, including dogs (*Canis familiaris*) (Miklösi et al., 1998; Range and Virányi, 2011; Téglás et al., 2012; Met et al., 2014; Duranton et al., 2017), birds (Watve et al., 2002; Bugnyar et al., 2004; Schloegl et al., 2007; Goossens et al., 2008; Jaime et al., 2009; Loretto et al., 2010; Kehmeier et al., 2011; Schmidt et al., 2011; Tornick et al., 2011; also see Kaplan, 2011; Nawroth et al., 2017), reptiles (Wilkinson et al., 2010; Simpson and O'Hara, 2019), and several primate species (e.g., Itakura, 1996; Emery et al., 1997; Tomasello et al., 1998; Anderson and Mitchell, 1999; Scerif et al., 2004; Bräuer et al., 2005; Burkart and Heschl, 2006; Shepherd and Platt, 2008; Ruiz et al., 2009; see Rosati and Hare, 2009, for a review; Sandel et al., 2011; Liebal and Kaminski, 2012; Chen et al., 2017; Drayton and Santos, 2017).

Clearly, gaze following does not necessarily imply complex cognition. Povinelli and Eddy, 1996, for instance, distinguished a low-level from a high-level form of gaze following in animals (also referred to as gaze following into space versus geometrical gaze following; see Loretto et al., 2010). In particular, low-level gaze following would be an innate response triggered by a shift in the individual's attention toward an external target: when a conspecific turns the head, for instance, the individual attention would be caught by this movement, and the individual would simply look in that direction, without any cognitive skills being involved. In contrast, high-level gaze following would also imply the ability to take others' perspective and thus understand what others see from their location: if the individual sees a conspecific looking in another direction, for example, it might use the conspecific's gaze as a cue to obtain information about the environment, eventually moving around barriers to gain the conspecific's perspective (Povinelli and Eddy, 1996).

Although gaze following appears to be widespread across taxa, at least in its lower-level form, some studies have shown important differences in gaze following behavior even among closely related species (Kano and Call, 2014). In particular, species can differ from each other in two main ways. First, they can differ in their general sensitivity to gaze following: while some species reliably follow others' gaze, others might be less sensitive to the gaze of others, and less reliably follow it. Stump-tailed macaques (*Macaca arctoides*), for instance, follow the gaze of conspecifics more frequently than other macaque species (Tomasello et al., 1998), while bonobos (*Pan paniscus*) are more likely to follow others' gaze, compared to chimpanzees (*Pan troglodytes*) (Herrmann et al., 2010; Kano and Call, 2014). Similarly, some species might avoid direct gaze and gaze following (see Kaplan and Rogers, 2002). Second, species can specifically differ in their ability to follow the gaze of individuals of other species (i.e., allospecifics). While the gaze of a conspecific might provide relevant information to individuals in most species (so that they would benefit from following it), allospecifics' gaze might less likely trigger gaze following behavior (see Kano and Call, 2014).

The reasons for these interspecific differences, however, are yet unclear. Some researchers, for instance, have proposed that differences in gaze following skills might depend on differences in motivation and/or selective interest in certain models (Kano and Call, 2014). Other researchers have rather highlighted the role of domestication in the emergence of gaze following skills (see Hemmer, 1990; Kaminski et al., 2005). On the one hand, domestication might reduce sensitivity to predators (because humans protect domesticated animals against other predators; Hemmer, 1990), so that gaze following might be less frequent in domesticated species, if its main function is the acquisition of information about the presence of predators (see Kaminski et al., 2005). On the other hand, domestication might have selected for especially tame and socially skilled individuals (e.g., Hare et al., 2002; Hare and Tomasello, 2005), which might have enhanced social cognitive skills, and also be better at following others' gaze. However, while some studies have suggested that domestication has a positive effect on species' ability to follow others' gaze (e.g., Kaminski et al., 2004), other researchers have found no positive effect of domestication on gaze following skills (e.g., Werhahn et al., 2016). Therefore, the effect of domestication on gaze following is yet unclear, and more comparative studies are required to better understand which factors best predict interspecific variation in gaze following (Kano and Call, 2014).

In this study, we aimed to compare species in their ability to follow the gaze of conspecifics and allospecifics and, in particular, the effect of domestication on these skills. For this purpose, we tested four different ungulate species: two domesticated ones (i.e., goats, *Capra aegagrus hircus*, and lamas, *Lama glama*), and two non-domesticated ones (i.e., mouflons, *Ovis orientalis orientalis*, and guanacos, *Lama guanicoe*). We selected ungulates for two main reasons. First, ungulates are a still largely understudied taxon, with only one species yet having been tested for its gaze following skills (Kaminski et al., 2005), to our knowledge. Therefore, testing these species can significantly increase the range of species on which we have information and help to shed light on the selective pressures that might affect the emergence of gaze following skills in different taxa. Second, ungulates include a variety of domesticated and non-domesticated species, with an impressive variety of socio-ecological characteristics (see Shultz and Dunbar, 2006). Therefore, they constitute an ideal model to contrast different evolutionary hypotheses on the emergence of gaze following skills.

Here, we used a consolidated experimental approach in which subjects observed either a conspecific or a human experimenter suddenly turning the head toward a distant location. We monitored whether subjects followed the conspecific's and the human's gaze, by turning the head in the same direction of the model, and whether species differed in their performance. We predicted that (1) all species would more likely follow the gaze of a conspecific (rather than a human), as individuals in all species should have more interest/motivation to obtain information from conspecifics than allospecifics (see Kano and Call, 2014). Moreover, we predicted that (2) both domesticated and non-domesticated species would show gaze following skills, as also shown in other taxa (e.g., Loretto et al., 2010; Wilkinson et al., 2010; Werhahn et al., 2016).

MATERIALS AND METHODS

Ethics

The Barcelona and Leipzig Zoos controlled and approved all the procedures. We used no invasive methods; individuals were never separated from their group and participated on a completely voluntary basis. During the task, individuals were never food or water deprived, and the tasks did not present any risks or adverse effects. Therefore, no formal approval was required.

Subjects

We tested 17 goats (*C. aegagrus hircus*) and 3 lamas (*L. glama*) housed at the Leipzig Zoo, and 4 guanacos (*L. guanicoe*), and 4 mouflons (*Ovis aries musimon*) housed at the Barcelona Zoo. Lamas and guanacos are phylogenetically closely related, and so are goats and mouflons, with lamas and goats having been domesticated approximately 5,000–3,800 and more than 10,000 years ago, respectively (see Vigne et al., 2005; Goñalons, 2008).

Study subjects included both males and females, and were all adults (i.e., older than one year), except for the goat sample, which also included four infants (for more details on the study subjects, see **Table 1**). The study subjects had little experience with experimental procedures: the lamas and some of the goats had been previously tested in a neophobia test (i.e., in which individuals were provided with food close to a novel object), while the guanacos and mouflons had never been taken part in any experiment. The tasks were carried out in the external facilities of the species, and their usual management was not changed due to our tasks. While goats and lamas are commonly considered domesticated species (Zeder and Hesse, 2000; Dong et al., 2015; Diaz-Lameiro, 2016), mouflons and guanacos are not (Lincoln, 1990; Cartajena et al., 2007; Chessa et al., 2009; Yacobaccio and Vilá, 2016).

Procedures

We administered two tasks, one using as a model a conspecific (Conspecific task), and one a human experimenter (Human task). We originally aimed to administer 6 to 12 trials per task and condition (i.e., Experimental and Control), but as subjects differed in their motivation to participate, the number of trials administered in each task and condition varied across them (see **Table 1**). Subjects were tested when they were approximately 1 to 4 m from the experimenter. All trials were video recorded with a video camera positioned just outside the ungulate enclosure, so that the subject was clearly visible. Subject responses were later coded from the videos (see below).

In the experimental condition of the conspecific task, we opportunistically waited for two individuals facing each other, one giving its back to the experimenter (i.e., subject) and one having the experimenter in his visual field (i.e., model; see **Figure 1A**). The experimenter tried to catch the model's attention (e.g., holding a piece of food in the air), so that the model would visibly move his head in another direction (e.g., raising or turning his head toward the experimenter), while the subject looked toward the model (i.e., so that the subject could see the model move his head). When the model moved the head toward the experimenter and the subject looked at the model, a trial was started. The control condition of the conspecific task was identical, except that no model was present, and the trial was started when the subject was giving his back to the experimenter (so that the subject was provided a no gaze cue; see **Figure 1B**). Trials were scored as successful if the subject turned his head in the same direction (i.e., at least 45°) in which the model looked at (for the control trials, in the direction in which the model looked at in the corresponding experimental trial).

In the experimental condition of the human task, we opportunistically waited for an individual (i.e., subject) to look at the experimenter (i.e., model; see **Figure 1C**). The model then suddenly raised his/her head toward a distant upper corner of the enclosure (either on the right or on the left, randomizing the side across subjects and trials), and a trial was started. The control condition of the human task was identical, except that the model raised his/her head toward the body of the subject (see **Figure 1D**). Trials were scored as successful if the subject turned his head toward the same upper corner of the enclosure (i.e., at least 45°) in which the model looked at (for the control trials, in the direction in which the model looked at in the corresponding experimental trial).

In both the conspecific and the human tasks, we first tested goats and lamas with 10-s trials. However, the greatest majority of subjects turned their head in the first 3 s of the experimental trials (i.e., 75% in lamas, 79% in goats). When testing guanacos and mouflons, therefore, we preferred to administer shorter trials (i.e., 3-s trials) to be more conservative (i.e., to avoid coding trials as positive when subjects moved the head for other reasons). Clearly, in order to ensure comparability across species, trials were coded as successful in all species and conditions if the response (see above) was given in the first 3 s. As all trials were video recorded and later scored from the videos (see above), the 3-s interval could be accurately measured from the videos.

Statistical Analyses

Analyses were conducted using generalized linear mixed models (Baayen et al., 2008) with the glmmTMB package (version 1.0.1; Brooks et al., 2017) in R (R Core Team, version 3.5.0). Our models were run with a binomial structure, entering one line per subject and trial, and further specifying whether the trial was successful (see above), the task and condition administered, the trial number, and the species, sex, and age of the subject. A second observer independently coded 20% of the videos (i.e., whether the

TABLE 1 | For each species, subjects participating in the task, including their sex and age class, and the number of trials in which they participated, for each task (conspecific and human) and condition (experimental and control).

Species	Subject	Age class	Sex	Number of administered trials			
				Consp. (exper.)	Consp. (control)	Human (exper.)	Human (control)
Goat	1	Adult	Female	3	3	4	6
	2	Adult	Female	0	0	3	2
	3	Adult	Female	0	0	5	5
	4	Adult	Female	0	0	4	4
	5	Infant	Female	0	0	6	6
	6	Infant	Female	0	0	5	2
	7	Adult	Female	1	1	5	6
	8	Adult	Female	0	0	6	6
	9	Adult	Female	1	1	6	6
	10	Adult	Female	6	3	6	5
	11	Infant	Male	0	0	2	2
	12	Adult	Female	0	0	6	6
	13	Adult	Female	4	4	5	5
	14	Infant	Male	0	0	4	5
	15	Adult	Female	1	3	3	5
	16	Adult	Female	1	2	6	6
	17	Adult	Male	1	1	6	6
Guanaco	Hembra abajo	Adult	Female	7	6	6	8
	Hembra arriba	Adult	Female	5	13	10	10
	Rojo	Adult	Male	6	7	8	8
	Verde	Adult	Male	6	6	7	8
Lama	Flax	Adult	Male	3	2	6	6
	Krümel	Adult	Male	3	3	6	6
	Sancho	Adult	Male	1	2	6	6
Mouflon	Circulo amarillo	Adult	Female	6	7	8	6
	Circulo naranja	Adult	Female	1	2	9	9
	Cuadrado blanco	Adult	Female	9	11	8	11
	Cuadrado rojo	Adult	Female	8	6	7	7
	Cuadrado verde	Adult	Female	6	4	9	12
	Macho	Adult	Male	6	4	7	10

trial was successful), and inter-observer reliability was excellent (Cohen's kappa = 0.94).

We then assessed whether the three-way interaction of species (as categorical predictor with four levels), task (two levels: conspecific and human) and condition (two levels: experimental and control) predicted subject's response (i.e., whether they would direct their gaze in the direction of the model's gaze, as explained above). In the model, we further included all the two-way interactions between species, task, and condition, and their main effects. We also included subject age and sex as controls (as in some species, gaze following skills are known to completely develop only by the end of infancy; e.g., Teufel et al., 2010; Rosati et al., 2016; and to be higher in females; e.g., Rosati et al., 2016). We finally included trial number as control (as response to others' gaze may vary through time, either increasing as a result of learning or decreasing as a result of habituation: Schloegl et al., 2007; Loretto et al., 2010), and subject identity as random factor.

We used likelihood ratio tests (Dobson et al., 2001) to compare the full model containing all predictors with the null model containing only control predictors and random factors. When the full model significantly differed from the null model, likelihood ratio tests were conducted to obtain the *p*-values for each test predictor via single-term deletion, using the R function drop1 (Barr et al., 2013). If the three-way interaction was not significant, we removed it from the full model and re-run the comparison with the null model by only including the two-way interaction of condition with species and condition with task, their main effects, control predictors, and the random factor. We detected no convergence issues. To rule out colinearity, we determined the VIFs (Field, 2005), which were minimal (maximum VIFs = 2.01).

RESULTS

The full-null model comparison was significant (GLMM: $\chi^2 = 76.61$, df = 15, $p < 0.001$). The two-way interactions between condition and task ($p < 0.001$) and condition and species ($p = 0.005$) were both significant. In particular, the study subjects looked in the model's direction more in the experimental than in the control condition in both tasks, although this difference

FIGURE 1 | Experimental setup for the two tasks and conditions: **(A)** Conspecific experimental trial. **(B)** Conspecific control trial. **(C)** Human experimental trial. **(D)** Human control trial. Continuous lines indicate the model's gaze direction, while dotted lines indicate subjects' gaze direction when trials were coded as positive.

was stronger in the conspecific task (conspecific task: $p < 0.001$; human task: $p = 0.016$; see **Table 2**). Moreover, while all species overall followed the model's gaze more in the experimental than in the control condition (see **Figure 2**), goats ($p < 0.001$), lamas ($p = 0.002$), and mouflons ($p < 0.001$) did it significantly so, but not guanacos ($p = 0.638$).

DISCUSSION

Our study provides the first experimental evidence of gaze following skills in non-domesticated ungulates. In line with our predictions, ungulates followed the model's gaze both with human and conspecific models, but were more likely to do so when the model belonged to the same species. Moreover, while all species followed the model's gaze more in the experimental than in the control conditions, non-domesticated guanacos failed to significantly do so (but see below for a better discussion on the relatively low sample size).

The main finding of our research is that gaze following skills are present in ungulates, even in non-domesticated species (i.e., mouflons). This is in line with previous studies in other taxa, which have already shown that non-domesticated species can reliably follow others' gaze (e.g., Loretto et al., 2010; Wilkinson et al., 2010), sometimes even better than their domesticated counterparts (e.g., Werhahn et al., 2016). Therefore, our study provides no support to the hypothesis that domesticated species show different gaze following skills than non-domesticated ones. Indeed, domesticated species do not seem to have a general advantage over non-domesticated species when following others' gaze (as expected if close co-evolution with humans during domestication had selected for socially skilled individuals; see Hare et al., 2002). Similarly, non-domesticated species do not seem to outperform domesticated ones (as expected if gaze following skills were less adaptive in domesticated species, which receive extensive protection from predators by humans; see Kaminski et al., 2005). In contrast, gaze following appears to be really widespread across taxa, at least in its simple forms.

In contrast to non-domesticated mouflons, however, non-domesticated guanacos failed to reliably follow the model's gaze, showing the same probability of gaze following in both experimental and control conditions. As visible in **Figure 2**, these results are mainly due to the low performance of guanacos (i.e., a higher proportion of successful trials in the control

TABLE 2 | Summary of the results for the full model, including the reference category for categorical predictors, estimates, standard errors (SE), *z*-values (*z*), confidence intervals (CIs), and *p*-values for each test predictor (in bold, when significant) and control predictor (in italics).

Predictors	Reference category	Estimate	SE	*z*	2.5% CI	97.5% CI	*P*
Intercept		−2.95	0.48	−6.13	−3.89	−2.01	
Species	Guanaco	2.17	0.52	4.15	1.15	3.20	
	Lama	1.05	0.72	1.46	−0.36	2.45	
	Mouflon	1.63	0.47	3.48	0.71	2.54	
Condition	Experimental	2.77	0.55	5.01	1.69	3.85	
Task	Human	1.08	0.34	3.15	0.41	1.75	
Species*condition	Guanaco, experimental	−1.82	0.56	−3.23	−2.93	−0.71	0.005*
	Lama, experimental	0.00	0.75	0.00	−1.47	1.47	
	Mouflon, experimental	−0.60	0.52	−1.16	−1.63	0.42	
Task*condition	Human, experimental	−1.54	0.45	−3.44	−2.42	−0.66	< 0.001*
Age class	Infant	−0.86	0.64	−1.35	−2.11	0.39	0.160
Sex	Male	−0.07	0.36	−0.21	−0.77	0.63	0.834
Trial		−0.02	0.04	−0.40	−0.10	0.07	0.693

The model had a binomial distribution and included subject identity as random effect. The asterisks denote significant p-values for the test predictors.

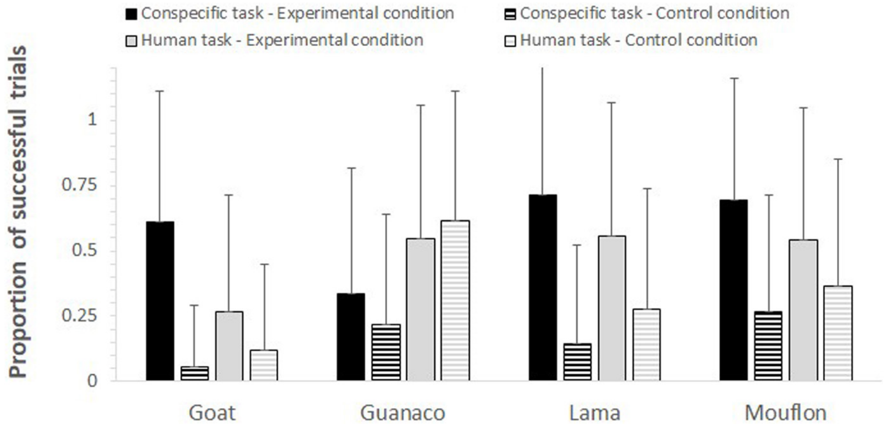

FIGURE 2 | For each species, task, and condition, the mean proportion (+SD) of trials in which subjects followed the model's gaze.

rather than experimental condition) when being tested with the human model. At the moment, it is not possible to understand why guanacos performed worse than the other species (including mouflons), especially with allospecific models. One reason might be that guanacos, for some yet unknown reason, show more selective attention toward their conspecifics, as chimpanzees also do (see Kano and Call, 2014). However, it is also simply possible that these results depend on our small sample size, as we could only test four guanacos. Although a larger sample size might have therefore provided different results, it is important to note that other species in our study showed evidence of gaze following skills, despite also having a small sample size (e.g., lamas, $N = 3$). Moreover, while the inclusion of more study subjects might show that also guanacos can follow the gaze of humans and conspecifics, this study already provides evidence that domestication is not necessary prerequisite for the emergence of gaze following skills in ungulates.

While it is true that guanacos performed especially poorly when tested with a human model, all species performed significantly worse when tested with humans rather than conspecifics. This seems to confirm that animals, either domesticated or not, generally have more interest and/or motivation to follow the gaze of conspecifics, as these can more likely provide relevant information (see Kano and Call, 2014). These findings have important implications for the study of interactions between humans and other animals. On the one side, they suggest an astonishing ability of most animal species (also non-domesticated ones) to use human gaze in the same way as conspecific gaze. On the other side, they suggest some limits in this ability, even in domesticated species.

Incidentally, sex, age, and trial number had no effect on individual performance in our study. These results are also largely in line with previous studies, which suggest that gaze following skills, at least in its lower-level form, emerge early on through development (see e.g., Kaminski et al., 2005; Range and Virányi, 2011). Moreover, as in previous studies (e.g., Kaminski et al., 2005), performance did not increase through time, suggesting that individual response was not the result of a learning process during the study.

Clearly, this study must be considered as a first attempt to study gaze following skills in ungulates. From a cognitive point of view, for instance, further research is needed to understand the psychological underpinnings of gaze following skills in the different species. By administering further conditions in which individuals need to take others' perspective to follow their gaze, we might be able to better understand whether ungulate species show high- or low-level forms of gaze following (see e.g., Amici et al., 2009; Loretto et al., 2010). Furthermore, future studies should include more individuals and species, to have more power, to better control for inter-individual differences and also to test other evolutionary hypotheses on the emergence of gaze following skills (e.g., high-level forms of gaze following are more likely to emerge in species with complex sociality; see e.g., Aureli et al., 2008; Dunbar, 2009). In the future, it will be especially important to also test other non-domesticated species. The ancestors of both guanacos and mouflons, for instance, have also been domesticated (i.e., into lamas and sheep; see e.g., Goñalons, 2008; Chessa et al., 2009; Alberto et al., 2018). Therefore, it is still possible that gaze following skills in these species are linked to the favorable pre-adaptive characteristics possessed by their ancestors, which might have favored their domestication, but also the emergence of social cognitive skills like gaze following (see e.g., Zeder, 2012). Finally, future studies should assess whether ungulate species differ in their sensitivity to the gaze of humans and conspecifics, depending on the context (e.g., competitive or cooperative; see Castellano-Navarro et al., unpublished). Overall, our study confirms ungulates as a promising taxon to study comparative cognition, and zoo-housed animals as ideal subjects to extend the range of tested species, also including those that have long been neglected in cognitive research (Nawroth et al., 2017).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because The Barcelona and Leipzig Zoos controlled and approved all the procedures. We used no invasive methods, individuals were never separated from their group and participated on a completely voluntary basis. During the task, individuals were never food or water deprived, and the tasks did not present any risks or adverse effects. Therefore, no formal approval was required. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

AS and AC collected the data, with support from MC, RH, and CE. AS, AC, and FA analyzed the data and wrote the manuscript, with extensive feedback from the other authors. All the authors designed the study together and contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.604904/full#supplementary-material

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Conflict of Interest: RH was employed by company Zoo Leipzig.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Context-Specific Arousal During Resting in Wolves and Dogs: Effects of Domestication?

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Due to domestication, dogs differ from wolves in the way they respond to their environment, including to humans. Selection for tameness and the associated changes to the autonomic nervous system (ANS) regulation have been proposed as the primary mechanisms of domestication. To test this idea, we compared two low-arousal states in equally raised and kept wolves and dogs: resting, a state close to being asleep, and inactive wakefulness, which together take up an important part in the time budgets of wolves and dogs. We measured arousal via cardiac output in three conditions: alone, with a familiar human partner, or with pack members (i.e., conspecifics). Specifically, we compared heart rate (HR) and heart rate variability (HRV) of six wolves and seven dogs. As patterns of resting can vary adaptively, even between closely related species, we predicted that dogs would be generally more aroused than wolves, because living with humans may come with less predictable contexts than living with conspecifics; hence, dogs would need to be responsive at all times. Furthermore, we predicted that due to the effects of domestication, emotional social support by familiar people would reduce arousal more in dogs than in equally human-socialized wolves, leading to more relaxed dogs than wolves when away from the pack. Overall, we found a clear effect of the interactions between species (i.e., wolf versus dog), arousal state (i.e., resting or awake inactive) and test conditions, on both HR and HRV. Wolves and dogs were more aroused when alone (i.e., higher HR and lower HRV) than when in the presence of conspecifics or a familiar human partner. Dogs were more relaxed than wolves when at rest and close to a familiar human but this difference disappeared when awake. In conclusion, instead of the expected distinct overall differences between wolves and dogs in ANS regulation, we rather found subtle context-specific responses, suggesting that such details are important in understanding the domestication process.

Keywords: heart rate, heart rate variability, dogs, wolves, domestication, dog-human relationship

INTRODUCTION

Domesticated species differ systematically from their wild conspecifics ("domestication syndrome," Darwin, 1859; Wilkins et al., 2014). As the primary domestication mechanism seems to be selection for tameness (Belyaev, 1979; Trut et al., 2004), domesticated animals have been suggested to be hypersocial – defined as "a heightened propensity to initiate social contact that often extends to members of others species" – toward other individuals, including humans, compared to their wild counterparts (vonHoldt et al., 2017). The dog-wolf model is a great system to investigate potential differences due to domestication. Dogs began to diverge genetically from wolves some 35,000 years ago (Frantz et al., 2016; Botigué et al., 2017). Domestication has affected the ecology and behavior of dogs (Axelsson et al., 2013; Miklósi and Topál, 2013; Range and Virányi, 2015; Marshall-Pescini et al., 2017; Kotrschal, 2018). Wolves are cooperative hunters and breeders which generally avoid close contact with humans (Mech and Boitani, 2003). Still, equally human-socialized wolves and dogs behave relatively similar in experimental situations. For example, they are attentive toward humans (Range and Virányi, 2013) and cooperate with them (Range et al., 2019b), greet familiar and unfamiliar humans (Hall et al., 2015; Ujfalussy et al., 2017), and like in dogs, their salivary cortisol decreases during training sessions (Vasconcellos et al., 2016). Human-socialized adult wolves maintain social bonds with their early caretakers and other familiar people (preprint; Wheat et al., 2020) and, hence, may benefit from their presence in stressful situations via emotional social support. Still, wolves may not depend on humans as much as dogs that are raised and kept in a similar way (Topál et al., 2005) because dogs usually live in human environments (Coppinger and Coppinger, 2001) and may be selected for attaching easily and strongly to their human caretakers (Palmer and Custance, 2008; Gácsi et al., 2013; Solomon et al., 2019).

Previous studies have shown a clear interaction between dogs' physiology and their emotional bonds with humans. For example, kennel dogs exposed to a novel environment in the presence of their human caretaker showed no increase in glucocorticoids, which was in contrast to when they were tested alone or with a familiar dog in a novel environment (Tuber et al., 1996). A study of pet dogs found that when dogs were petted by their owner during a veterinary examination dogs' heart rate and ocular surface temperature increased less than when facing examination alone (Csoltova et al., 2017). Furthermore, another study of pet dogs showed that dogs' heart rate variability (HRV) generally increased in response to being pet by their owners (Katayama et al., 2016), which suggests that this is experienced as a positive and rewarding situation. In humans also, heart rate and HRV is linked to emotional responses (Porges, 1995; Appelhans and Luecken, 2006).

The autonomic nervous system (ANS) regulates the heart and other visceral functions (Shields, 1993), including the expression of emotions in the social context (Porges, 2003). As domesticated animals differ from their wild ancestors mainly in their emotional responses to human contexts, domestication may have affected ANS modulations, the more as the neural crest hypothesis suggests that 'initial selection for tameness leads to a change in the neural-crest-derived tissues' (Wilkins et al., 2014), which includes the ANS. In turn, this leads to the changes observed trough all domesticated species, the so called "domestication syndrome" (Darwin, 1859; Wilkins et al., 2014).

The modulation of the ANS can be estimated via cardiac activity (Porges, 1995, 2001, 2003, 2009; Rajendra Acharya et al., 2006; Kreibig, 2010). Useful parameters are HR, i.e., the number of heartbeats per time unit, and HRV, i.e., the variation over time of the period between consecutive heartbeats (R-R intervals). While both physical activity and mental states modulate HR (Visser et al., 2002; Maros et al., 2008), HRV is less dependent on physical activity than HR, but generally decreases via psychological stress and increases during relaxation (Luque-Casado et al., 2013). A way to avoid the effect of physical activity on ANS modulation and thus, cardiac outputs, and test the emotional effect of social support by a social partner on wolves and dogs is to compare their arousal at rest.

Rest is considered as an intermediate state of the sleep-wakefulness continuum (Campbell and Tobler, 1984) defined as, "a state of reduced activity without the loss of consciousness or greatly reduced responsiveness" (Lesku et al., 2006; Siegel, 2008). At rest, parasympathetic activity increases, resulting in a comparatively low HR and high HRV. In addition, respiration deepens in association with a sinusoid pattern of HR, which is caused by the rhythmic breathing of the animal. This is called respiratory sinus arrhythmia (RSA, Oken et al., 2006). As RSA is present in both wolves (Kreeger et al., 1990) and dogs (Hamlin et al., 1966), we used it as a marker of a deep state of relaxation, i.e., resting (Kortekaas and Kotrschal, 2019). In the present study, we focused on the resting state but we also included a state in which an animal is more aroused and alert than during rest, i.e., the awake inactive state in which an animal is paying close attention to its environment (Oken et al., 2006) but is still physically inactive. With the term "arousal," we integrate correlated mental and physiological states; low arousal such as during rest is equivalent to decreased consciousness toward environmental stimuli, with relatively low HR and high HRV.

Not much is known about dog resting patterns; they probably change with age, environment, and social context as it has been observed with sleep patterns. For example, living conditions affected the length of dog sleep cycles and the time they spent sleeping (Adams and Johnson, 1993) as shelter dogs slept more but with shorter sleep cycles than dogs living with owners. Interestingly, if more than one dog lived in the same household, the dogs tended to show asynchronous sleep-wake cycles (Adams and Johnson, 1993), meaning that at least one of them was awake at any time. Other studies have shown that after an active day, dogs are drowsier earlier and sleep more (Bunford et al., 2018) and older dogs sleep more during the day and less at night than younger dogs (Takeuchi and Harada, 2002; Bódizs et al., 2020). Also, the frequency of sleep spindles (i.e., a burst of brain activity) has been shown to vary with age, physical activity, social pre-sleep activity, sex, and reproductive status (Kis et al., 2014, 2017; Iotchev et al., 2019), factors which also have been shown to affect the HR and HRV of dogs before falling asleep (Varga et al., 2018). In adaptation to different ecologies and lifestyles, sleep patterns may vary substantially, even among closely related species (Siegel, 2005; Lesku et al., 2008; Aulsebrook et al., 2016). For example, birds (gadwall and black-tailed Godwit) had their eyes open for longer periods of time during rest/sleep when in large groups or in the center of the flock (Gauthier-Clerc et al., 2000; Dominguez, 2003). Whereas in yellow baboons, individuals in smaller groups were resting higher above ground than individuals in bigger groups (Stacey, 1986). Socialized wolves, were found to be more relaxed than dogs and have lower HR and higher HRV during periods of rest and inactive wakefulness (Kortekaas and Kotrschal, 2019). This has been suggested to be a specific adaptation of dogs for living in a human environment, which is presumably less predictable than the pack environment of wolves and hence, would necessitate a greater basic alertness. However, in this study, an unfamiliar human was present during the recording of the animals' behavior, which might have influenced the results.

In our present study we assessed the effect of domestication on the modulation of dogs' ANS by comparing wolves' and dogs' ANS modulation in three different social conditions: alone, with a familiar human, and with the other pack members. Similar to Kortekaas and Kotrschal (2019), we investigated two behavioral states with minimal physical activity and sensory stimulation: resting (animal is lying immobile and eyes closed) and inactive wakefulness (animal is lying with its head in an upward position with the eyes open). We compared cardiac output in similarly raised and kept, and therefore fully comparable, group-living wolves and dogs. We selected periods of respiratory sinus arrhythmia for analysis, as this is indicative of rest (Kortekaas and Kotrschal, 2019).

As human-socialized wolves form social bonds with familiar humans, we expected that emotional support by humans would modulate their ANS. However, due to dogs' adaptation to the human environment during domestication, the proposed emotional support effect should be more pronounced in dogs than wolves. Different predictions can be generated from the major dog domestication hypotheses. If selection for tameness as primary mechanism of domestication (Belyaev, 1979; Wilkins et al., 2014) shaped dogs' ANS's modulation, we predicted they would be generally more relaxed (i.e., less reactive to stressful events and with lower HR and higher HRV) than their wild ancestors (Darwin, 1868; Price, 1999; Hare et al., 2012). Based on the hypersociality hypothesis (vonHoldt et al., 2017), we expected that dogs would benefit more (i.e., be more relaxed at rest and with lower HR and higher HRV compared to a control condition where the animals are alone) in the presence of a human and possibly also in the presence of conspecifics than wolves. Alternatively, the intention to interact with the familiar person or pack member – due to the proposed higher sociability of dogs as compared to wolves – might result in increased arousal (higher HR and lower HRV). However, this was not expected to be the case once the animals has settled down to rest.

In contrast to the precedent domestication hypotheses, the canine cooperation hypothesis (Range and Virányi, 2015) suggests that dogs' social and cooperative skills toward humans are not a by-product of domestication but rather a direct wolf heritage originating from the wolves' social orientation toward pack members. This hypothesis suggests that during domestication dogs shifted their cooperative orientation to humans. Based on this hypothesis we predicted that wolves as well as dogs would relax in the presence of both a familiar human and a conspecific pack member. This is in alignment with the deferential hypothesis (Range et al., 2019b), which predicts that dogs should benefit more from the human presence than wolves, dogs should gain a greater support effect from humans (i.e., lower HR and higher HRV with a human compared to being with other dogs) whereas wolves would gain great support effect from conspecifics (i.e., lower HR and higher HRV with their conspecifics). In contrast to the hypersociability hypothesis (vonHoldt et al., 2017), the deferential hypothesis would not predict that dogs can benefit more from the presence of other dogs.

MATERIALS AND METHODS

Ethical Approval

This research was approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-11/11/2018).

All study animals were housed at the Wolf Science Center (WSC) located in the Game Park Ernstbrunn in Austria. Their participation in the experimental sessions was voluntary. If they were not motivated to leave their home enclosure, the session was canceled and repeated on a different day. In nine cases, trials had to be repeated for this reason. If the subject did not rest in the test enclosure during the session, the condition was repeated on another day, in total this situation happened 53 times. If they did not rest in five sessions, the subject was tested in its home enclosure while its pack mates were brought to the test enclosure ($n = 2$). Via these adjustments we also achieved a homogenous motivational basis for our experiments. Only animals in a positive/relaxed mood would participate, because temporarily wary or anxious animals would not leave their enclosure to participate. All animals at the WSC are well habituated to being shifted to and from their home enclosure and also to experimental procedures.

Subjects

Subjects were six wolves, *Canis lupus* (three males and three females) and seven dogs, *Canis lupus familiaris* (four males and three females; see **Table 1**). All wolves and dogs were born in captivity and were hand-raised from 10 days old by humans following a standardized procedure to produce trustful and workable partners for research (Klinghammer and Goodman, 1987). At 5 months of age they were integrated into preexisting conspecific packs. For more details on the raising of the animals see Range and Virányi (2014).

All animals were kept in small groups in outside enclosures ranging between 2,000 and 8,000 m^2 in size with natural landscape including trees, bushes, shelters, and natural objects such as stones, branches, and tree trunks. The subjects were between 5 and 11 years of age when tested – wolves: median (range) = 7 (6–10); dogs: median (range) = 4 (4–8) and had between 20.8 and 48.9 kg – wolves: median (range) = 40 (37.5–48.9); dogs: median (range) = 24.5 (20.8–35). The wolves were fed with carcasses of deer, rabbit, or chicken 3–4 times a week, while the dogs were fed with commercial dog food daily. As the dogs could not be provided carcasses, like the wolves, the dogs were regularly provided food enrichment, such as small pieces of deer, rabbit, or chicken, to make wolf and dog feeding as similar as possible. Water was available *ad libitum* to all wolves

TABLE 1 | List of the subjects.

Individual	Species	Sex	Date of birth	Weight*	Pack size
Amarok	Wolf	♂	4.04.2012	39.82	2
Aragorn	Wolf	♂	4.05.2008	48.50	3
Chitto	Wolf	♂	4.04.2012	46.72	2
Shima	Wolf	♀	4.05.2008	39.50	2
Tala	Wolf	♀	4.04.2012	39.15	2
Yukon	Wolf	♀	2.05.2009	37.82	3
Enzi	Dog	♂	2.04.2014	29.00	4
Gombo	Dog	♂	21.03.2014	28.67	2
Hiari	Dog	♂	21.03.2014	24.13	3
Imara	Dog	♀	21.04.2014	21.39	3
Meru	Dog	♂	1.10.2010	24.18	2
Panya	Dog	♀	2.04.2014	25.20	4
Zuri	Dog	♀	24.05.2011	20.80	4

**Weights displayed here are the weights of the subjects over the three testing days in kilograms.*

and dogs, including during training and test situations. Wolves and dogs had the same amount of contact with humans and both received veterinary and obedience training from puppyhood and cooperated in a number of behavioral tests on a weekly basis. As a result, all animals were accustomed to participating in research while separated from their pack members.

Data Collection

Overall, we tried to keep our methods as similar as possible to Kortekaas and Kotrschal (2019). Heart rate (HR) was measured via the Polar®RS800CX system designed for human usage. The accuracy of the Polar system has been validated for dogs via a comparison with a conventional electrocardiogram (ECG; Jonckheer-Sheehy et al., 2012; Essner et al., 2013, 2015). The system consists of a chest belt with electrodes, which are fastened around the animals' chest behind the shoulders. From there the data are sent to a watch-like data logger attached to a neck collar. As the belt was designed for humans, the fur of the wolves and dogs impedes the belt electrodes. Hence, the fur under the electrodes in the belt was wetted with 70% ethanol to enhance signal conductivity. The entire procedure was trained beforehand via positive reinforcement.

HR data were first checked for the presence of respiratory sinus arrhythmia as an indicator of deep rest (i.e., a sleep-like condition). Video recordings of these sessions were coded with Solomon Coder©. HR and behavioral data were manually synchronized. Specifically, when the watch started recording data, the experimenter said loudly "start," which was used as a signal for synchronizing the video and the HR recording. For the resting condition, all HR data showing a respiratory sinus arrhythmia pattern and the matching resting behaviors was kept. For analyses, HR and HRV recording are required to be the same length of time to be comparable (von Borell et al., 2007). Most of our animals rested for more than 80 s but for one wolf (Amarok resting with a familiar human) and one dog (Enzi resting alone) 80 s was the shortest maximum time they spend resting. Hence, we selected 80 s HR strands for analysis and all bouts shorter than 80 s were excluded from further analyses. One resting bout was randomly selected per animal and conditions. For the inactive wakefulness, no specific HR pattern has been described (in analogy to RSA during rest), hence we selected any strand of HR data longer than 80 s that corresponded to awake but inactive behaviors (i.e., laying down immobile with eyes open). If the animal moved (i.e., changed the position of its body or its head) or closed its eyes for more than a blink (i.e., eyes closed for more than 1 s and opening again, 1 s corresponded to five frames on Solomon Coder) the HR strand was discarded. One strand of HR per animal and activity (i.e., resting or inactive wakefulness) was randomly selected. As we only had one HR recording per animal and condition, we avoided selecting multiple strands of the same activity (i.e., resting or inactive wakefulness) to avoid dependent data points.

HR measurements collected with the Polar system can contain artifacts, leading to the need for editing (von Borell et al., 2007). Accordingly, the HRs measured were corrected using the algorithm-supported visual error correction (AVEC) method (Schöberl et al., 2015), applying a confidence interval for the outliers of 95%. HR measurements with more than 5% of errors were excluded. Heart rate variability (HRV) in this study was expressed as the root mean square of successive differences (RMSSD), normally used for short-term HRV analysis (for RMSSD details see von Borell et al., 2007). Mean HR and RMSSD were calculated with Kubios©. Resting HRs and awake inactive HRs were taken from the same recording but were not time adjacent.

Procedure

The experimental sessions were conducted during a quiet period of the day when the animals were resting (normally between 12 am and 2 pm). Depending on the condition, the focal subject was taken out of the pack and brought to a test enclosure with some distance to its home pack or was accommodated in the shifting system immediately adjacent to the pack enclosure (i.e., the subject was only separated from the pack mates by a single wire mesh). Before the onset of the experimental phase, an animal trainer applied the Polar-belt to the subject for the recording of the HR. During the test period (1 h), no human was present around the enclosure (i.e., keeping away from the enclosure and out of sight of the animal tested) except for the human company condition. Each session was recorded with one or two cameras (depending on the size and configuration of the enclosure).

The animals were tested in the following three conditions: (1) alone: the subject was alone in its enclosure; (2) human company: The subject was alone in its enclosure while a familiar human was sitting just outside the fence of the enclosure (minimal distance 50 cm). The subject was free to approach the human or to stay away. The familiar human was instructed to not interact with the subject, but instead was reading a book or working on a laptop; (3) conspecific company: The subject and its pack members (1–3) stayed in visual contact during the test hour but were separated by a fence.

We analyzed cardiac outputs in two different behavioral conditions, resting and inactive wakefulness. We used the same behavioral criteria as Kortekaas and Kotrschal (2019) to define two conditions.

1. Resting: The body touching the ground either with caudal, dorsal, or lateral side. The position of the paws varies, e.g., folded (under body) or stretched out. The head is in a downward position, either lying on paws, ground, or tucked under the body. The eyes are generally closed but may repeatedly open and close (peeking). Parts of the body occasionally twitching.
2. Inactive wakefulness: The subject is awake, body touching the ground either with caudal, dorsal, or lateral side. The position of the paws varies, e.g., folded (under body) or stretched out. The head is in an upward position and can be moved around. The eyes are open, but increased blinking can occur.

Statistical Analyses

All models were fitted in R (version 3.6.1; R Core Team, 2019) using the function lmer of the R package lme4 (version 1.1-21; Bates et al., 2014). To test whether the cardiac parameters would differ depending on species, activity of the subject, and condition of the test, the response variables "mean" HR and RMSSD (a common measure for HRV) were both analyzed in separate linear mixed effect models (LME, Baayen, 2008). Species (wolf or dog), activity (resting or inactive wakefulness), condition of the test (alone, with a human, or with conspecifics) included as fixed effects factors. We also included in the model a three-way interaction between species, activity and condition (and also all three two-way interactions this encompasses) in order to understand how cardiac outputs changed as a function of activities and conditions and how these differences in cardiac outputs varied between wolves and dogs. To control for the effects of temperature, body mass, age, and sex, these factors were also included as fixed effects. Subject identity was included as a random intercept to account for individual differences and to avoid pseudo replication, as all subject were tested in each condition. To keep type I error rates at the nominal level of 5%, we included random slopes of condition and activity and also the correlation parameters among the random intercept and random slopes terms of the HR model (Schielzeth and Forstmeier, 2009; Barr et al., 2013). However, we chose to exclude those correlations from the HRV model because many of them were estimated to be close to 1 or −1 which is indicative of them to be unidentifiable (Matuschek et al., 2017). This led to an only moderate decrease in model fit (HRV model with correlations: logLik = −440.3498 (*df* = 32) and HRV model without correlations: logLik = −446.6024 (*df* = 22). Body mass, age, and temperature were z-transformed (to a mean of zero and a standard deviation of one). Activity, condition, and species were manually dummy-coded (i.e., the categorical predictors were replaced by one or several dummy variables, one for each level of the factor except its reference category, each consisting solely of 0 and 1 s to facilitate model computation) and then centered to a mean of zero before including them in the random slopes in the model.

We checked whether the residuals were normally distributed and homogeneous by visually inspecting a qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations from these assumptions. We checked for model stability by excluding subjects one at a time from the data and comparing the model estimates derived for these subsets of the data with those derived for the full data set. Both models were unstable for the factor species (see **Supplementary Tables 1**, **2**). To check for potential collinearity issues, we inspected Variance Inflation Factors (VIF, Field, 2005) which we derived using the function VIF of the R-package car (Fox and Weisberg, 2018), applied to a standard linear model excluding the random effects and interactions. This revealed that species and body mass were slightly collinear with a VIF of 11.57 and 10.21, respectively. However, there was considerable variation of body mass within both species and, hence, the results obtained for these two predictors should not be distorted by collinearity among them.

To avoid cryptic multiple testing and keep type I error rate at the nominal level of 0.05 (Forstmeier and Schielzeth, 2011) we tested the significance of the full model as compared to the null model (comprising only age, body mass, sex, temperature, and the random effects) by means of a likelihood ratio test (R function anova with argument test set to "Chisq"; Dobson and Barnett, 2018). To allow for a likelihood ratio test we fitted the models using maximum likelihood (rather than Restricted Maximum Likelihood; Bolker et al., 2009). *P*-values for the individual effects were based on likelihood ratio tests comparing the full with the respective reduced models (Barr et al., 2013; R function drop1).

The sample size for both these models was 73 observations made on 13 individuals (seven dogs, six wolves). Six data points were missing as the animals did not display the behaviors measured in this study (rest/inactive wakefulness). Four data points were included despites displaying bad RSA pattern to enhance model stability (Meru alone, Zuri alone and with human company, Hiari alone).

RESULTS

Mean Heart Rate

Overall, species, activity, and condition had a clear effect on HR (full-null comparison likelihood ratio test: $\chi^2 = 57.22$, $df = 11$, $P < 0.001$). More specifically, we found that the interaction between species, activity, and condition had an effect on HR ($\chi^2 = 10.60$, $df = 2$, $P = 0.005$; **Table 2**) and that the HR differences between dogs and wolves varied depending on the combination of test conditions and activities.

Overall, HR in wolves and dogs was lower when resting, as compared to being awake but inactive (**Figures 1A,B**). During rest, dogs in proximity of a social partner (human or conspecific) had lower HRs than when alone (**Figure 1A** and **Table 3**). In contrast, during inactive wakefulness, dogs' HRs in proximity of a familiar human were higher than in the two other conditions (**Figure 1B**) and dogs' HRs when alone or with conspecifics was similar. During rest, the HRs of wolves were lower in proximity to their pack members as compared to being close to a familiar human or alone (**Figure 1A**). In addition, wolf HRs seemed

TABLE 2 | Results of the HR Model.

	Estimate	SE	χ^2	F	P[1]
Intercept	97.245	6.440			
Species (0, dog; 1, wolf)	−25.237	9.604			
Human	9.908	4.123			
Conspecifics	3.002	5.315			
Activity (0, awake; 1, rest)	−11.773	3.560			
Body mass[2]	10.706	3.585	5.187	1	**0.023**
Temperature[2]	−2.027	1.016	3.378	1	0.066
Age[2]	15.248	2.402	14.648	1	**<0.001**
Sex (0, F; 1, M)	−5.251	2.470	3.015	1	0.082
Wolf:Human	−21.823	6.053			
Wolf:Conspecifics	−16.729	7.465			
Wolf:Rest	−7.956	4.942			
Human:Rest	−9.627	4.448			
Conspecifics:Rest	−7.030	4.361			
Wolf:Human:Rest	22.889	6.490	10.601	2	**0.005**[3]
Wolf:Conspecifics:Rest	10.030	6.185			

Statistically significant p-value are in bold.

[1] *Not indicated in the case where p-value had a limited interpretation.*

[2] *Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD) were weight: 32.98 (9.49) kg, temperature: 22.41 (7.18)°C and age 2440.23 (801.93) days.*

[3] *Overall test of the three-way interaction between species, activity and conditions.*

similar when resting alone or in proximity of a familiar human (**Figure 1A** and **Table 3**). When awake and inactive, wolf HRs near a pack member were lower as compared to being alone or close to a familiar human (**Figure 1B**). Furthermore, HRs of wolves and dogs were roughly similar when resting near their pack members whereas they differed in the two other conditions (**Figure 1A**): Dog HRs were lower than those of wolves when alone or close to a human partner (**Figure 1A**). During inactive wakefulness wolves had higher HRs than dogs when alone whereas in the social conditions the HRs of wolves and dogs were similar (**Figure 1B**). HRs also increased with age (estimate ± SE = 15.24 ± 2.40, $\chi^2 = 14.65$, $P < 0.001$) and body mass (estimate ± SE = 10.71 ± 3.59, $\chi^2 = 5.19$, $P = 0.023$), whereas sex and temperature had no significant effect (**Table 3** and **Supplementary Table 1**).

We found distinct inter-individual differences in HR in both dogs and wolves (see **Supplementary Figure 1**). In the dogs, two subjects seemed to drive the decrease in HR at rest, whereas two other animals had the highest HR during the pack condition. In the inactive but awake state, two individuals had the highest HRs in presence of a familiar human (**Supplementary Figure 1A**). Similarly, in the wolves, two animals displayed a higher HR when resting with a familiar human than when alone, whereas one female had a substantially lower HR in presence of a familiar human than when alone. Only one wolf had a higher HR when with her pack than when alone. During inactive wakefulness, two individuals had very high HRs when alone and for both of them the presence of a familiar human seemed to lead to a lower HR. Compared to the alone condition, all wolves displayed lower HRs in the presence of their pack mates; however, when compared to the human condition, two wolves had higher HRs and two lower HRs in the pack condition (**Supplementary Figure 1B**).

Heart Rate Variability (RMSSD)

Overall, the full model was significant as compared to the null model (likelihood ratio test: $\chi^2 = 40.15$, $df = 11$, $P < 0.001$), i.e., species, activity, condition, or their interaction(s) affected the root mean square of successive differences (RMSSD, which expresses heart rate variability; HRV) in wolves and dogs. However, since the three-way interaction between species, activity, and condition was not significant (likelihood ratio test: $\chi^2 = 3.47$, $df = 2$, $P = 0.18$, **Figures 1C,D** and **Table 3**), we removed it from the model to explore the significance of the two-way interactions between our factors of interest: species, activity and condition. The two-way interaction between species and condition was significant (likelihood ration test: $\chi^2 = 8.48$, $df = 2$, $P = 0.014$); wolf and dog RMSSDs were similar in the alone condition, but in presence of a social partner dogs had higher HRVs than wolves (**Supplementary Figure 2**). Also, the two-way interaction between species and activity was significant (likelihood ration test: $\chi^2 = 8.27$, $df = 1$, $P = 0.004$), meaning that both wolves and dogs had similar RMSSDs when awake and inactive while at rest dogs had higher RMSSDs (**Supplementary Figure 3**). Finally, the two-way interaction between activity and condition was also significant (likelihood ratio test: $\chi^2 = 7.99$, $df = 2$, $P = 0.018$). When alone RMSSDs of wolves and dogs did not differ much between being awake or resting, whereas when with a social partner (human or conspecifics) RMSSDs where higher at rest than when awake (**Figures 1C,D**). RMSSDs decreased with age (estimate ± SE = −103.54 ± 41.19, $\chi^2 = 5.07$, $df = 1$, $P = 0.024$) whereas body mass, sex, and temperature had no significant effect on the RMSSD (**Table 4** and **Supplementary Table 2**).

As the case with HR, we also found considerable individual differences in RMSSD. In two dogs it was overall lower than in the other dogs at rest. Also, individual dogs differed in their response to the presence of their pack; when resting two individuals had substantially lower RMSSDs close to their pack as compared to being alone, while during inactive wakefulness three individuals had higher RMSSDs with their pack as compared to the alone condition (**Supplementary Figure 1C**). At rest, two wolves, did not vary in their RMSSD, regardless of condition. During inactive wakefulness, the RMSSD of three wolves reached lowest values in the presence of the familiar human, whereas it peaked in two others in this condition (**Supplementary Figure 1D**).

DISCUSSION

Our results show than dogs and wolves' cardiac output varies with degree of activity, social environment, and also quite substantially between individuals in the different contexts. Across all three conditions, both wolves and dogs were less aroused, showing lower heart rates (HR) and higher heart rate variation (HRV) when resting, as compared to inactive wakefulness. This aligns with previous results (Varga et al., 2018; Kortekaas and Kotrschal, 2019). However, in contrast to Kortekaas and Kotrschal (2019),

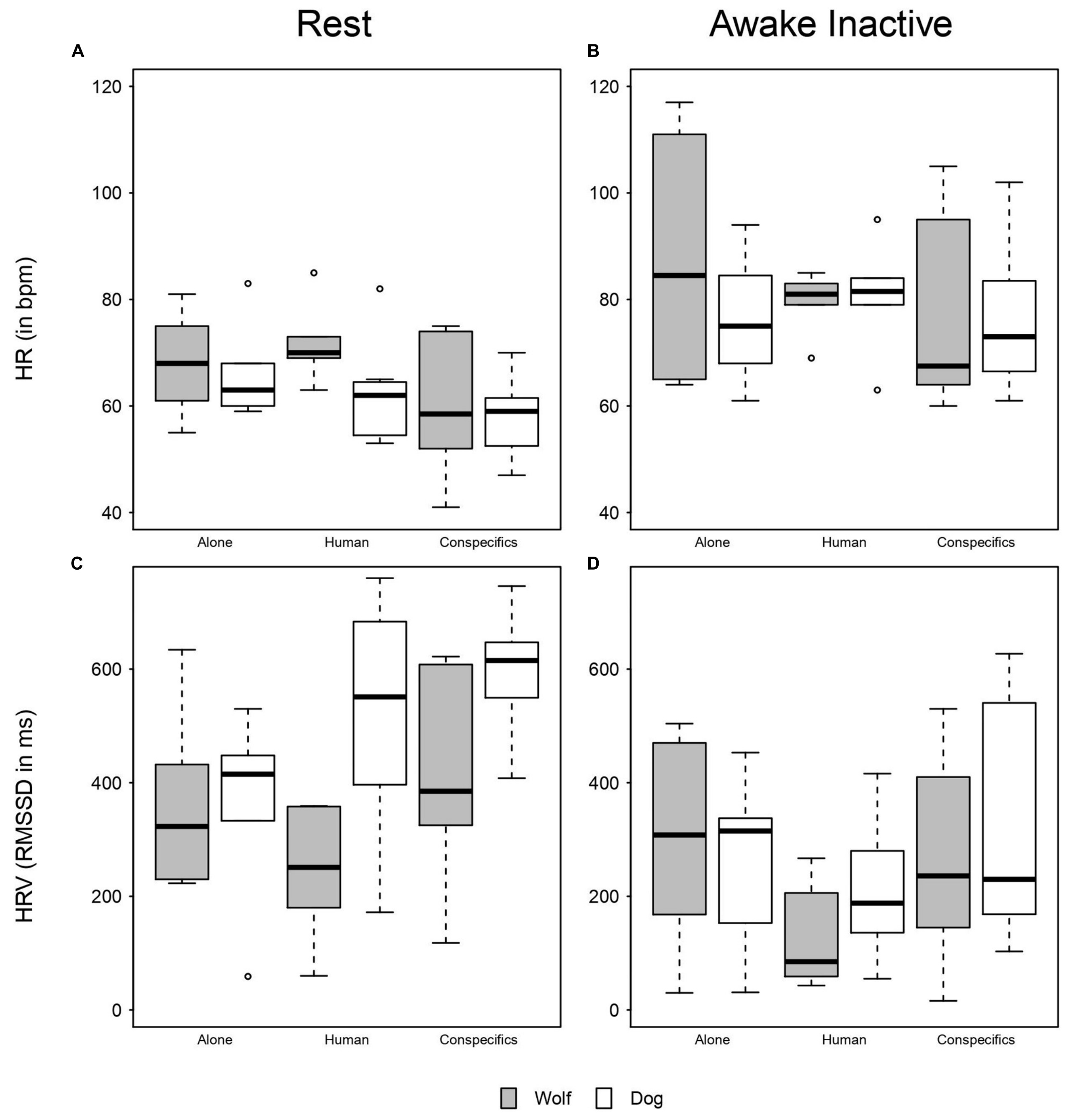

FIGURE 1 | Boxplot of mean HR and HRV. **(A)** Mean HR of wolves and dogs when resting across conditions. **(B)** Mean HR of wolves and dogs when awake and inactive across conditions. **(C)** HRV of wolves and dogs when resting across conditions. **(D)** HRV of wolves and dogs when awake and inactive across conditions.

dogs at rest were generally less aroused (i.e., had lower HR and higher HRV) than wolves but showed roughly the same cardiac parameters as wolves when awake and inactive. This discrepancy may be explained by the different social context in the two studies. Kortekaas and Kotrschal (2019) had an unfamiliar human filming all the experimental sessions, while in our study we controlled for familiarity by having either no human, a familiar human, or conspecifics nearby. The presence of an unfamiliar human could have been more arousing than soothing for the dogs than the presence of a familiar human. However, we also need to note that as we found a substantial individual variation in our data, the differences between the two studies might also be explained by small samples sizes, as discussed below.

Interestingly, we found that dogs at rest seemed to respond to the presence of a familiar human in a similar way as to

TABLE 3 | Descriptive statistics for the mean HR and RMSSD values.

			HR					RMSSD				
Species	**Condition**	**Activity**	**Mean**	**SD**	**Min**	**Max**	**Median**	**Mean**	**SD**	**Min**	**Max**	**Median**
Dog	Alone	Rest	66.60	9.81	55	81	63	357.00	180.94	59	530	415
Dog	Alone	Awake	76.43	12.80	64	117	75	254.28	152.96	31	453	315
Dog	Human	Rest	62.14	10.09	53	82	62	520.43	225.84	172	760	551
Dog	Human	Awake	80.67	10.33	63	95	81.5	210.50	128.53	55	416	188
Dog	Conspecific	Rest	57.71	8.03	47	70	59	594.57	113.53	408	746	615
Dog	Conspecific	Awake	76.57	14.73	61	102	73	339.71	222.21	103	627	230
Wolf	Alone	Rest	68.00	10.08	59	83	68	360.84	155.22	223	634	323
Wolf	Alone	Awake	87.67	23.15	61	94	84.5	298.00	189.20	30	504	308
Wolf	Human	Rest	72.00	8.12	63	85	70	241.60	126.68	60	359	251
Wolf	Human	Awake	79.40	6.23	69	85	81	132.00	98.94	43	267	85
Wolf	Conspecific	Rest	59.84	13.23	41	75	58.5	407.17	189.96	118	622	385
Wolf	Conspecific	Awake	76.50	18.81	60	105	67.5	262.17	185.56	16	530	236

Descriptive statistics of dogs and wolves mean HR and RMSSD values grouped by conditions and activity.

TABLE 4 | Results for the HRV model.

	Estimate	**SE**	χ^2	***df***	**P**[1]
Intercept	270.451	88.462			
Species (0: dog; 1: wolf)	80.431	133.413			
Human	−24.868	57.153			
Conspecifics	122.402	44.987			
Activity (0: awake; 1: rest)	149.889	43.636			
Body mass[2]	80.874	60.934	1.567	1	0.211
Temperature[2]	−5.988	14.578	0.162	1	0.688
Age[2]	−103.540	41.188	5.072	1	**0.024**
Sex (0: F; 1:M)	−68.764	69.425	0.973	1	0.324
Wolf:Human	−163.474	76.643	8.478	2	**0.014**[3]
Wolf:Conspecifics	−168.204	53.965			
Wolf:Rest	−130.650	42.885	8.266	1	**0.004**
Human:Rest	150.712	53.755	7.994	2	**0.018**[4]
Conspecifics:Rest	114.564	51.403			

Significant p-value are in bold.

[1] *Not indicated in the case where p-value had a limited interpretation.*

[2] *Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD) were weight: 32.98 (9.49) kg, temperature: 22.41 (7.18)°C and age 2440.23 (801.93) days.*

[3] *Overall test of the two-way interaction between species and conditions.*

[4] *Overall test of the two-way interaction between activity and conditions.*

the presence of their pack members (i.e., lower HR and higher HRV than when alone), whereas in our human-socialized wolves, pack members seemed to be more effective at being emotional social support than familiar humans. When dogs and wolves were awake, the differences between their cardiac parameters decreased, probably because both were more alert (increased HR and lower HRV) as compared to resting with eyes closed. More specifically, when awake and close to a familiar human, the HRs of our human-socialized wolves and dogs were similar, whereas the HRVs were still lower in wolves. Also, during inactive wakefulness, the dogs had distinctly higher HRs and lower HRVs in the presence of a familiar human than when alone or with pack members, whereas differences between conditions were less clear in the wolves. It seems that the presence of humans affected dogs differently depending on if the dogs were awake, where multiple other stimuli may influence them and reduce the effect of the human, or asleep when there were fewer external stimuli to distract the dogs. We suggest that when awake, the dogs anticipated interacting with the familiar human, which may have increased their arousal. Wolves showed similar arousal levels than dogs in the presence of familiar humans as indicated by similar HR but HRV in this condition was lower in wolves than in dogs. As HRV has been linked to cognitive processes (Maros et al., 2008; Luque-Casado et al., 2013), we speculate that the presence of familiar humans might have been cognitively more stimulating for the wolves than for the dogs. Alternatively, due to the presence of a close human partner, our socialized wolves could have also anticipated interesting events, such as a test situation, training session, or a social interaction, whereas the dogs may have responded with relatively unspecific excitement. In other words, our socialized wolves may attribute a different meaning or valence (HRV is frequently used to assess affective state; Kreibig, 2010) to the presence of a human than the dogs. Still, these wolves are similarly attentive to humans than the dogs (Range and Virányi, 2011), benefit from training interactions with them in a similar way (Vasconcellos et al., 2016), and interact socially with their hand-raiser (Ujfalussy et al., 2017). Our socialized wolves also differed in their HRV responses to the presence of a familiar person, which hints at the importance of the quality of social relationships and personality.

Rather than dogs being overall calmer than wolves due to domestication (Hare et al., 2012) or being "hypersocial" (vonHoldt et al., 2017), our results support the idea that pack members act as social support in wolves and that dogs use humans similarly as social support (Range and Virányi, 2015). This seemingly minor shift in the social significance of conspecific pack members versus socialized humans may have far-reaching implications. Support by a familiar human – in most cases the owner – can indeed help dogs to cope with a task or an unfamiliar situation (Topál et al., 1997; Gácsi et al., 2013; Horn et al., 2013). Comparable studies with human-socialized wolves are essentially lacking: Topál et al. (2005) found that, unlike

16 weeks old dogs, 16 weeks old hand-reared wolves did not show a preference for a human caretaker in an Ainsworth's strange situation test. However, these wolves were not intensively in contact with their caretaker at the period the test was conducted (Virányi et al., 2008). Hence, as the wolves' and dogs' socialization substantially differed between research groups, results are hard to compare. Hall et al. (2015) found that socialized wolf puppies at 3, 5, and 7 weeks of age showed attachment behavior to a human caregiver. However, proper comparisons of wolves with dogs require similarly socialized and reared animals, as, for example, available at the WSC. A recent preprint, and hence not peer-reviewed study, comparing similarly reared wolves and dogs found that both species showed attachment toward their caretakers as adults (preprint; Wheat et al., 2020).

Our data also conforms to our daily experience with the WSC wolves and dogs; both show signs of attachment to familiar persons/their hand raisers and dogs tend to be generally more excited in the presence of such a person, while wolves behave in a relatively calm and focused way. Therefore, we suggest that the different ways dogs and wolves relate to humans as social partners also influences the way they cooperate with them but wolves and similarly raised dogs have probably more in common than they would differ in this respect. For example, in both wolves and dogs, attentiveness and willingness of the animal partners to cooperate seems to depend on relationship quality (Auer et al., 2011) and in both, successful cooperation generates a positive feedback on the social relationships between a human and a companion animal and reduces salivary cortisol (Vasconcellos et al., 2016). In fact, it has been demonstrated in a range of experiments that human-socialized wolves do cooperate with humans in a similar way than dogs (Range et al., 2019a,b) but subtle differences remain. For example, when given the choice, wolves tend to initiate and lead in such interspecies-cooperation, whereas dogs rather tend to follow the leading human and in general, the willingness of wolves to cooperate with humans seems to depend even more on relationship quality in wolves than in dogs (Range et al., 2019b).

Our data indicate strong potential effects of social relationships (with the human or the conspecifics present) as well as age, weight, and previous experience on the cardiac responses in the different contexts. This is not surprising, as individual bonds with both different humans and conspecifics differ in quality (Cimarelli et al., 2019). We suggest that this is an important underlying factor for much of the inter-individual variation found. In addition, personality is likely to be important. For example, during a safe haven test, reactive dogs (i.e., dogs prone to vocalizing when separated from their owner or growl and bark when approach by a threatening stranger) displayed HR and HRV changes during the test whereas the non-reactive dogs did not (Gácsi et al., 2013). Our moderate sample sizes in combination with relatively complex modeling did not allow us to include these potential causes of variability as factors but they should be kept in mind for future studies.

As age and weight may affect cardiac parameters, we will shortly discuss them here. In humans, HR generally increases in old age (Landowne et al., 1955; Umetani et al., 1998) but evidence for this in animals across their "normal" adult age range is rare, even more so in canids (Hezzell et al., 2013). As generally true for mammals, HR will decrease from puppyhood into adulthood in wolves and dogs, and may increase again in old age animals, mainly due to deteriorating health (Mosier, 1989; Strasser et al., 1997; Ferasin et al., 2010; Hezzell et al., 2013). Even less clear are the potential interactions between weight and cardiac responses in dogs. As HR in mammals is generally negatively correlated with body mass (Brody, 1945), this may also be true for dogs (Kirkwood, 1985; Sutter et al., 2007). However, most previous studies in dogs failed to demonstrate this (Ferasin et al., 2010; Lamb et al., 2010; Nganvongpanit et al., 2011; Rishniw et al., 2012). Hezzell et al. (2013) indeed found that HR scaled negatively with body mass, whereas Hamlin et al. (1967) reported that Great Danes HR frequencies exceeded that of miniature poodles. A recent study contributes to these contrasting results by reporting only a limited effect of body mass on HR (Cruz Aleixo et al., 2017). We presently controlled for body mass and age by adding them into the statistical model and found an influence of body mass on HR, while age affected both HR and HRV. Since wolves were heavier and older than the dogs in our study, the two variables could also have a confounding effect, e.g., if HR would increase with increasing age, this would also explain the body mass effect on HR. This is supported by Kortekaas and Kotrschal (2019), who also controlled for age and weight effects on cardiac output and found none. In their study, wolves were heavier but dogs and wolves were similar in age. Hence, in our study a confounding effect of age and weight is likely. We have no reason to assume a linear increase of HR with age over adulthood (Mosier, 1989; Strasser et al., 1997), the more as all our experimental animals were adults in good health, receiving regular veterinary care. Although we controlled for age and weight, we still found an effect of species, condition, and activity on HR and HRV. Hence, age and weight do not seem to explain much of the variability in our data. We therefore conclude that despite the differences in wolf and dog body mass and age, our comparisons of HR over different contexts are still valid. Such concerns do not affect HRV in a similar way as this parameter seems even more independent of body size or motor activity than HR (Cruz Aleixo et al., 2017).

We are aware that our relatively moderate sample sizes of six wolves and seven dogs, in combination with rather complex statistical models, do not allow us to draw final conclusion on the nature of wolves' and dogs' context-specific cardiac outputs. However, the cardiac parameters measured hint at a potential domestication-related difference in context-specific ANS modulation between wolves and dogs. Whether these results in our pack-kept dogs are representative also for pet dogs remains unclear but we suggest that the patterns we found are probably generic for human-socialized wolves and dogs and hence, would also be valid for pet dogs.

To conclude, wolves' and dogs' alertness and relaxation levels partially differed according to context. When resting, dogs more than wolves seemed to rely on human as social support, whereas when awake we measured similar cardiac responses to human proximity. This suggests that ANS modulation of dogs may be affected by domestication in a more complex way than suggested by simplistic interpretations of the selection-for-tameness hypothesis of domestication.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-11/11/2018).

AUTHOR CONTRIBUTIONS

HJ-J, KKor, and KKot designed the experiments. HJ-J wrote the manuscript, collected the data, and analyzed them. KKor, FR, and KKot revised the manuscript. All authors have contributed to, seen, and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.568199/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Manipulable Object and Human Contact: Preference and Modulation of Emotional States in Weaned Pigs

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Enriching the life of farm animals is a legal obligation in intensive farming conditions in the European Union, though not worldwide. In pigs, manipulable materials are mandatory when no bedding is available. Like manipulable objects, positive human interactions might also be considered as enrichment, as they provide the animals with opportunities to interact, increase their activity and lead to positive emotional states. In this study, we investigated how weaned pigs perceived an inanimate manipulable object and a familiar human. After a similar (in length, frequency, and procedure) familiarization to both stimuli, 24 weaned pigs were tested for a potential preference for one of the stimuli and submitted to isolation/reunion tests to evaluate the emotional value of the stimuli. We hypothesized that being reunited with a stimulus would attenuate the stress of social isolation and promote a positive state, especially if the stimulus had a positive emotional value for pigs. Although our behavioral data showed no evidence that pigs spent more time close to, or in contact with, one of the stimuli during a choice test, pigs more often approached the human and were observed lying down only near the human. Using behavioral and bioacoustic data from isolation/reunion tests, we showed that a reunion with the human decreased the time spent in an attentive state and mobility of pigs to a greater extent than a reunion with the object, or isolation. Vocalizations differed between reunions with the object and the human, and were different from those during isolation. The human and object presence led to higher frequency range and more noisy grunts, but only the human led to the production of positive shorter grunts, usually associated with positive situations. In conclusion, pigs seemed to be in a more positive emotional state, or be reassured, in the presence of a familiar human compared to the object after a short period of social isolation. This confirms the potential need for positive pseudo-social interactions with a human to enrich the pigs' environment, at least in or after potentially stressful situations.

Keywords: enrichment, welfare, emotional reactivity, human-animal relationship, behavior, acoustic communication

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INTRODUCTION

An intensive production system for animal products sometimes implies high densities of farm animals and can lead to deleterious behaviors and decrease their physical or mental health, i.e., their welfare.

Animal welfare covers, among other things, the importance of the animal's ability to control its mental and physiological stability in different environmental conditions (1). Improving animal welfare involves both reducing negatively perceived contexts as well as increasing positively perceived contexts and species-specific behaviors (2, 3). The pressure from citizens, consumers, and animal welfare organizations regarding animal rights has been growing, leading to changes in the legislation. For example, the provision of manipulable materials to pigs of all ages has been mandatory in the European Union since January 2013 (4), using materials named as "environmental enrichments." Environmental enrichments are defined as materials which can improve the biological functioning of captive animals (5) and should stimulate their species-typical sensory systems, cognitive capacities and behaviors (6). For instance, enrichments materials for pigs should be edible, chewable, investigable, and manipulable [(7) reviewed in (8)]. Moreover, enrichment materials should be provided in such a way that they offer sustainable attraction for pigs, should be accessible for oral manipulation, and provided in sufficient amount (5, 8). Enrichment effects are generally tested using behavioral and physiological paradigms (9) and are classified as optimal (if they meet all of the above-mentioned criteria), suboptimal (if meet most of the criteria but should be combined with other enrichment materials) or marginal [if they do not fulfill the animals' needs and should only be used with other enrichment materials (8)].

In the particular case of pigs, abnormal patterns of behavior (stereotypies, belly nosing, ear, and tail biting) may arise at several stages of their development if they are devoid of any enrichment (10). Enrichments have the potential to reduce these abnormal behaviors and increase positive behaviors like play (11, 12). Although straw bedding is one optimal enrichment according to literature [reviewed in (8)], it is laborious and costly to implement for farms using fully slatted floors. Thus, other manipulable materials in the form of ropes, hanging balls, wood, pipes, or different commercial toys have been developed and are used in farms.

Besides these enrichment materials, one may wonder if enrichment can be provided by other stimuli in the environment of farm animals. As pigs are social animals, social enrichment is sometimes used for nursing piglets, by allowing different litters to interact. This enrichment enhances play and decreases aggression at weaning (13). Another relational partner of pigs is their caregiver. Human interactions seem to correspond well to the definition of enrichment, i.e., they provide occasions of contact with another animal (stimulating biological functioning), and stimulate all sensory systems of the animals. Humans, notably through their clothes and boots, are chewable, investigable, and manipulable. Many beneficial outcomes of positive human interactions have been shown. Farm animals may be tamed by humans providing regular additional positive contacts, leading to the expression of positive emotions (14). Humans may consequently be associated with positive outcomes as measured by a decrease of heart rate (15–17), higher heart rate variability and indicative ear postures [ears hanging (17)], as well as their EEG [lower EEG total power and a shift in spectral power distribution toward higher frequencies (18)]. Humans can also acquire reassuring properties in situations of social isolation (19, 20). They may even induce behavioral reactions similar to those toward social partners (21). Cognitive bias tests showed a positive judgment bias in piglets that had received gentle contacts with humans (22). As positive judgment bias is often used to qualify the emotional state, this indicates that regular positive human contacts may lead to improved welfare. In addition, pigs raised in a poor environment may develop more interest toward a familiar human than pigs raised in an enriched environment (23), leading the author of the study to hypothesize that a familiar human may be perceived as an enrichment. To our knowledge, no comparison exists of the effect of inanimate object enrichment and pseudo-social enrichment via human interactions. This would provide new insight into enrichment practices for welfare improvement in pig breeding.

In this study, we developed a paradigm to test the perception pigs may have toward two stimuli: an inanimate object that could be used as enrichment, and a familiar human. The aim of this study was thus to elucidate the specific value for enrichment that a familiar human may have compared to an inanimate object. After familiarizing the pigs with each of them, we first evaluated the potential preference for one of the stimuli and then evaluated the emotional value of the stimuli through isolation/reunion tests. We hypothesized that being reunited with a stimulus would attenuate the stress of social isolation and promote positive behaviors (attraction toward the stimulus, contacts with the stimulus, play behaviors), especially if the stimulus has a higher positive emotional value for pigs. We used behavioral and bioacoustic data known to be relevant in comparing emotional states of pigs (24–26). Additionally, we tested if the level of attraction toward the stimuli could predict vocal expression in the presence of each stimulus.

MATERIALS AND METHODS

Ethical Note

The experiment was carried out at the experimental farm UEPR, in Saint-Gilles, France, under the authorization no. APAFIS#17071-2018101016045373_V3 from the French Ministry of Higher Education, Research and Innovation, received after evaluation by the regional ethics committee (Comité Rennais d'Ethique en Experimentation Animale), and conformed with the French and European legislation regarding experiments on animals.

Animals and Experimental Conditions

Twenty-four healthy weaned female pigs (Landrace/Large white dams inseminated with Piétrain semen) were involved in total. Pigs were weaned at 28 days of age. Eight groups of three sister pigs from eight different sows were selected at weaning according to their weight (the weight was balanced between and within the groups, 9.05± 0.66 kg on average). Thus, only familiar pigs from the same genetic mother were put together in rearing pens. Groups were housed in the same rearing room, in 115 × 132 cm pens, with slatted flooring, visually isolated from each other by 1.5 m high plastic panels. Pigs were fed *ad libitum* and had continuous access to a water trough. Each pen was provided with a steel chain as enrichment [mandatory by the Council Directive 2008/120/EC 2008 but demonstrated as low quality enrichment

(8)]. The pigs were involved in the experiment from 28 to 57 days of age.

For several phases of the experiment, we also used an experimental room. This was located in the same building as the rearing room, 15 m away, and was a 270 cm × 270 cm soundproof room. It was warmed by an electric heater. The entrance door was equipped with a hatch for the pigs. The transportation from the rearing room to the experimental room was done by the usual caretakers in closed trolleys. We used visually isolated trolleys to transport either the group of three pigs together (L120 × W80 × H80 cm), if they were brought to the experimental room all together (familiarization sessions with stimuli in the experimental room, see below), or one pig for a time (L80 × W50 × H80 cm), if the pigs were brought to the experimental room for a test (Choice test and Isolation/Reunion test, see below).

Human and Object Familiarization

All the pigs were familiarized with two stimuli: an experimenter, subsequently referred to as "Human" (always the same person, a 1.65 m tall woman dressed in a blue overall) and a 5L-plastic can (L20 × W10 × H30 cm), filled with water, from which hung three pipe pieces tied with a thin rope so that the three pigs could all chew it together, subsequently referred to as "Object." The Object thus met some of the criteria for an enrichment material, such as chewable and manipulable, but not other criteria like edible and destructible. Human and object familiarization sessions were alternated. Familiarizations started at 28 days of age and ended at 53 days of age. They were divided into two phases for each stimulus: eight sessions in the home pen (from days 29 to 35), and eight sessions in the experimental room (from days 36 to 43 and 49 to 53). In the home pen, each group of three pigs received 10 min sessions twice a day for each stimulus for 4 days. During the same week, all groups were alternately transported to the empty experimental room and remained there for 10 min, once a day for 5 days, to become habituated to the new room. After this habituation, pigs received 10 min sessions of stimulus familiarization in the experimental room, once a day for each stimulus, for 9 days. The same procedure was used for each group of three pen mates, as follows:

- Object: the experimenter came to the gate of the pen holding the object and stood still and quiet for 30 s. Then, she entered the pen to tie the object to the opposite wall with a small rope and went out. From the moment she went out, the object was left for 10 min in the pen. Then the experimenter removed the object.
- Human: the experimenter came to the gate of the pen, holding a 40 cm high stool, and stood still and quiet for 30 s. She then entered to sit on the stool in the pen, close to the opposite. To minimize stress on the first day (day of weaning, day 28) the human engaged in no interaction. From 29 days of age, during each session, she engaged in interactions with each pig [similar to the protocol in (16)]: she held out a hand toward the pig; if the pig did not move away, she tried to touch it; if the pig accepted being touched, she softly stroked it along the body with the palm of her hand; once it accepted being stroked, she scratched it along the body with her fingers. Scratching consisted of rubbing the skin of the pigs with the finger tips and applying more pressure than stroking. In addition, the handler spoke to the pig with a soft voice. The experimenter focused on each pig for 2 min initially and alternately focused her attention during the last 4 min.

The procedure of familiarization was similar in rearing pens and in the experimental room, but the location of the stimulus changed: in rearing pens, the stimulus was attached to the opposite wall from the entrance of the pen. In the experimental room, the stimulus was placed in the center of the room.

Choice Test

Experimental Procedure

At 47 and 49 days, the pigs were subjected to an individual Choice test between the familiar experimenter and the familiar object, in order to evaluate the potential preference for one of the stimuli. The test took place in the experimental room fitted with a V shaped arena (**Figure 1A**). The room was, as much as possible, made symmetrical with a false heater and camera, and a homogeneous ground surfacing. On the previous day, pigs were individually left in this room for 5 min in order to become habituated to the room and to being transported alone in a trolley. On the day of the test, the pigs were brought individually to the entrance of the experimental room. Once in front of the experimental room, the hatch to the room and the first hatch of the trolley were opened for 30 s. Since the trolley had another grid hatch, the tested pig could initially see into the experimental room without entering it. The human and the object were already in place at the back of the room (**Figure 1A**). The caretaker then opened the grid hatch and gently pushed the pig into the room if it had not entered by itself after 2 s. The Choice test lasted 5 min. The experimenter actively called the pig to come to her during the test. If the pig came close, the experimenter petted it, as in the familiarization sessions. This test was done twice, on consecutive days, swapping the sides of the stimuli between days in order to take into account possible bias due to the laterality of the apparatus or the pigs.

Behavioral Observations and Analyses

The tests were video recorded by a camera (Bosh, Box 960H-CDD) and a recorder (Noldus Mpeg recorder 2.1., The Netherlands), linked to a LCD monitor (DELL 48 model 1907FPc) which allowed us to visualize the experimental room from an adjacent room. The location of the pigs was monitored directly during the tests and the other behaviors later from videos, both using The Observer XT 14.0 software (Noldus®, The Netherlands). All behaviors recorded are indicated in **Table 1** and correspond to the behavior code numbers: 2–7, 11, 14 (restricted to stimulus zone) and 16.

Isolation/Reunion Test

Experimental Procedure

At 55, 56, and 57 days of age, pigs were subjected to an Isolation/Reunion test in order to assess their perception of each stimulus and its potential to calm the pigs after a period of stressful isolation (**Figure 1B**). The test consisted in two phases. The pig was brought individually in a trolley to the experimental

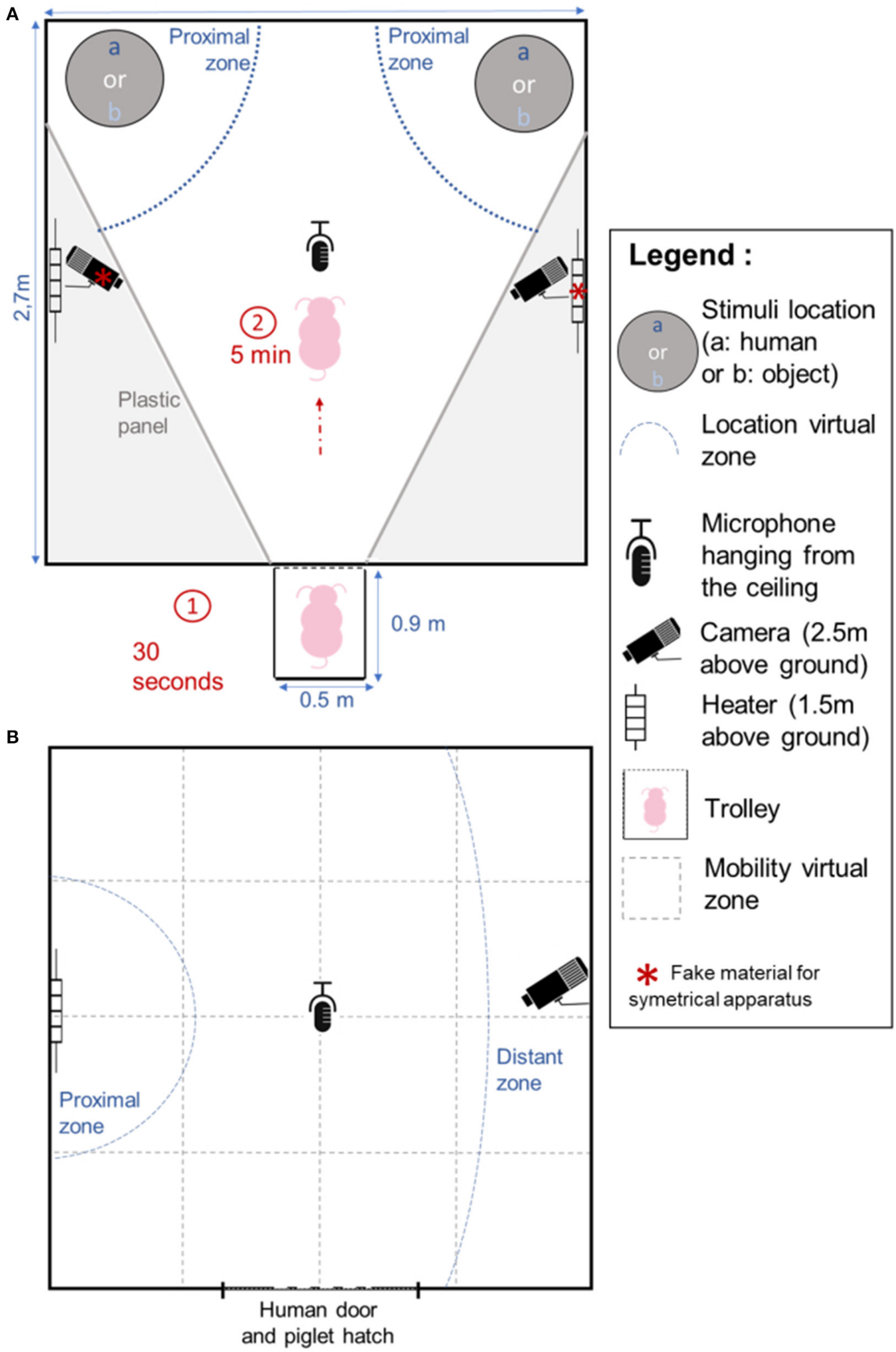

FIGURE 1 | Design of the experimental apparatus for the Choice test **(A)** and the Isolation/Reunion test **(B)**. For the Choice test between Object and Human **(A)**, each pig remained in the trolley for 30 s before entering the room where it was left for 5 min. For the Isolation/Reunion test **(B)**, the pig was left alone for 5 min (Isolation phase), and then remained for 4 min and 30 s (Reunion phase) either alone, with the familiar inanimate Object or with the familiar Human, on different days. Proximal zones: blue solid lines were drawn to identify the zones in which the pig was considered close to the stimulus. The distant zone **(B)** was drawn to identify a zone where the pig was considered distant from the stimulus. Virtual zones were drawn to monitor the location and mobility of the pig in the room (gray dotted lines).

TABLE 1 | Ethogram used for the Choice test (1), Isolation/Reunion test (2), and behavioral proximity scores (3).

Behavior	Description	Parameter (1: Choice test, 2: Isolation/Reunion test, 3: Behavioral proximity score)	References
Location of the pig Located in a virtual zone	The pig is considered in a virtual zone when its forelegs and head are in the zone	Number of changes (2)	(1)
Located in stimulus zone	The animal is considered in a zone when its forelegs and head are in the zone	Number of times (1, 3)	(2)
		Mean duration (1, 3)	(3)
		Total time (1, 3)	(4)
		First approach (Human vs. Object)	(5)
		Proportion of time (1)	(6)
		Latency to first entrance (1, 3)	(7)
Located in proximal zone	The pig is considered in the proximal zone when its forelegs and head are in the zone	Total time (2)	(8)
		Latency to first entrance (2)	(9)
Located in distal zone	The pig is considered in the distal zone when its forelegs and head are in the zone	Total time (2)	(10)
Postures Lying	The pig is lying ventrally or on the flanks	Presence or absence during test	(11)
Standing immobile	The pig is standing still, head up but not oriented toward the entrance door	Total time (3)	(12)
Looking at exit door	The pig is standing still, head turned toward the entrance door	Total time (3)	(13)
Exploring	The pig is sniffing or investigating a part of the environment, wall, or ground, with the snout	Total time (1, 2)	(14)
Contacts Initiated contacts toward a stimulus	The pig initiates a contact to the stimulus (by head or any body part)	Number of times (3)	(15)
		Total time (1, 3)	(17)
Contact received by the experimenter	The pig is gentled (scratched, stroked) by the experimenter, but did not initiate the contact	Number of times (3)	(18)
		Total time (3)	(19)

Columns describe the name of the behavior, its description, the parameters calculated with it and for which test it was used. A number was assigned to each behavior for reference. The unit for timing is the second, except when it is labeled with a "" for which it is standardized per minute.*

room, the hatches were opened and the pig was gently pushed into the room. It was left alone for five min, which defined the "Isolation" phase. Then, one of the stimuli ("Human," "Object") or "Nothing" was shown to the pig for 30 s: the door was opened with either: (a) the human standing with the stool, (b) the human standing with the object, or (c) nothing presented. Finally, the second phase named "Reunion" phase occurred and consisted of either (a) presence of the experimenter sitting in the room on a stool and remaining immobile and quiet ("Human" stimulus), (b) presence of the object tied in the room (i.e., "Object" stimulus: the human had to enter the room, install the object, and leave the room), or (c) isolation in the room for 270 s ("No stimulus"). Each pig was thus tested three times, with one test per pig per day. The order of the modalities (reunion with human, object or without stimulus) was randomized between days and between pigs of the same pen.

Behavioral Observation and Analyses

The same equipment as for the Choice test was used for the Isolation/Reunion test (see section above), but different behaviors were scored. All behaviors used are indicated in **Table 1** and correspond to the behavior code numbers: 1, 8–10, 14.

Acoustic Monitoring and Analyses

Vocalizations produced during the Isolation/Reunion test were recorded with a C314 microphone (AKG, Austria) placed in the center of the room at a height of one meter, connected to a MD661MK2 recorder (Marantz, USA). The vocal types were then manually annotated (grunt, squeak, bark, scream, and mixed calls), after visual inspection of spectrograms on Praat® software, by an expert [call types in pigs have been described and grunts are particularly typical low frequency and noisy calls (27, 28)]. Only grunts were subsequently acoustically analyzed as they represented the most frequent call type that constituted a dataset of 5,766 calls. A spectro-temporal analysis was performed with custom-written codes using the Seewave R package (29) implemented in R (30). After a 0.2–8 kHz bandpass filtering ("fir" function), a standardized grunt was detected when the amplitude crossed a 5% amplitude threshold ("timer" function) to measure call duration. After amplitude normalization, the following spectral parameters were calculated ["specprop" function, FFT with Hamming window, window length = 512, overlap = 50%): mean, median, first (Q25) and third (Q75) quartiles, interquartile range (IQR), centroid (all in Hz)]. The grunt dominant frequency (in kHz) was also calculated ("dfreq," 50% overlapping FFTs, window length = 512), which is the mean over the call duration of the frequencies of the highest level of energy. Parameters measuring noisiness and entropy of the grunt were: Shannon entropy (sh), Spectral Flatness (Wiener entropy, sfm) and Entropy (H) [combining both Shannon entropy and Temporal envelop entropy, length = 512, Hilbert envelop].

Statistical Analyses

All the statistical analyses were done using R 3.3.3 (30). Synthetic variables were built with Principal Component Analyses (PCA) and models were constructed to test the effect of the factors of interest. Linear or generalized mixed effect models ("lmer" or "glmer" function, "lme4" R package) were used to test two-way interactions between factors and/or continuous covariates; the pig's identity was put as a random factor (repeated measures per pig) in all models, as nesting individuals within pens (nested random effect) did not lead to converging models.

Analysis of Choice Test: Spatial Behavior of Pigs

To be able to assess and compare the behaviors during the 5 min of the Choice test and reduce the number of tested variables, a Principal Component Analysis (PCA) was done considering all behaviors directed toward each stimulus [parameters: 2–7, 11, 14 (restricted to stimulus zone) and 16, **Table 1**] (31). All PCs having an Eigen value above one were kept and constituted three behavioral response scores, which cumulatively explained 81.3 % of the variability (choicePC1−46%, choicePC2−20%, choicePC3−16%, variable loadings, **Table 2**). The absolute values of each parameter, in several relevant conditions of the study are available in **Supplementary Table 1**. The three behavioral response scores were used as response variables in linear models testing the interacting effect of the day of the test (two levels: first or second) and the stimulus (two levels Human vs. Object); the position of the human (left or right) was added as a control for choices linked to laterality (model 1). Two additional behaviors were tested as binary variables: the first approach (Human or Object, parameter code 5, **Table 1**) and whether the pig laid down near one stimulus (presence or absence, parameter code 11, **Table 1**). To test whether the first approach depended on a stimulus, it was tested in a binomial model (Human or Object) and the effect of the day and the position of the human were put in an additive model (model 2). The number of times a pig laid down in the proximal zone close to a stimulus was tested as a binomial variable (presence vs. absence) and a χ^2 test was used.

TABLE 2 | Variable loadings of the behavioral parameters used in the Principal Component Analysis in the Choice test.

	Percentage per PC			Relative cumulative values		
	choicePC1	**choicePC2**	**choicePC3**	**choicePC1**	**choicePC2**	**choicePC3**
Cumulative inertia	45.8	65.3	81.3	–	–	–
Number of visits in stimulus zone	0.63	60.90	1.84	−2.03	82.86	2.07
Mean duration in stimulus zone	24.19	11.56	1.49	−77.59	−15.73	−1.68
Proportion of time in stimulus zone	23.76	4.38	0.15	−76.21	5.95	0.17
Time spent in contact with the stimulus	22.06	3.22	0.01	−70.77	−4.38	−0.01
Time spent exploring when in stimulus zone	0.22	17.21	37.35	−0.70	23.41	−41.97
Latency to approach zone	0.90	1.62	59.12	2.89	−2.21	−66.44
Total time in zone	28.25	1.11	0.03	−90.64	1.51	−0.04

All Principal components (PCs) having an Eigen value above one were kept to build behavioral response scores. The first line of the table indicates the cumulative inertia explained by the PCs. For each PC, the percentage of (left side) as well as the relative cumulative value (right side) of a given parameter is indicated. Parameters having a percentage above the uniform distribution can be considered as explanatory parameters for a given PC.

Analysis of Isolation/Reunion Tests: Spatial and Vocal Behavior of Pigs

Behavioral response scores

To be able to have comparable behaviors, between phases and stimuli, and to reduce the number of variables, behaviors were gathered and a PCA was computed (parameter codes: 1, 8–10, 14, **Table 1**) (31). Only parameters measurable in any condition (phase of the test and type of reunion) were kept and the percentage of explained variance maximized. All PCs having an Eigen value above one were kept and constituted three behavioral response scores, which cumulatively explained 82% of the variability (IsoReuPC1—32%, IsoReuPC2—39%, IsoReuPC3—11%, variable loadings, **Table 3**). The absolute values of each parameter, in relevant groups of the study are available in **Supplementary Table 2**.

Acoustic scores

To be able to compare the spectro-temporal structure of grunts, two scores were built. The duration of grunts was log transformed and used as a temporal score (linear distribution). For spectral analysis, parameters previously extracted were gathered in a PCA to be able to monitor which parameters load the same way and build an acoustic score. Only one PC had an Eigen value above one, explained 83% of the variability and was named "Acoustic spectral score (PCac.)." The absolute values of each parameter, in relevant groups of the study, are available in **Supplementary Table 3**.

Statistical models

The three behavioral response scores (IsoReuPC1, IsoReuPC2, IsoReuPC3) and the two acoustic scores [PCac. and log(duration)] were used as response variables in a linear model testing (i) the two-way interaction between the type of reunion (Human/Object/No stimulus) and the phase of the test (Isolation/Reunion), (ii) the two-way interaction between the day of the test (1/2/3) and the phase, (iii) the day of the test and the type of reunion (model 3).

Analyses of Predictors for Vocal Expression During the Reunion With the Stimulus

The aim of this analysis was to search for the best predictors of vocal dynamic and grunt acoustic features, in the presence of the human or the object. For this analysis, only the dataset containing the reunion phases with the Human or the Object were used, extracted from the Isolation/Reunion test.

Monitoring spatial proximity toward the stimulus and time during the test

The location of the pig in the room was divided into two categories: when the pig was located in the proximal zone ("Close") and when the pig was located elsewhere ("Away") to build a two level factor named "Location." This parameter allowed us to track for *spatial proximity* toward the stimulus. Each period of time that the pig was Close or Away was considered as a time interval. Each time interval was numbered to track the rank of the interval during the test and the "Interval index" variable was created (e.g., Close1, Away2, Close3…).

Building behavioral proximity scores toward the stimulus

Using the behavioral observations during the Choice test, *behavioral proximity scores* reflecting the closeness and exploration toward each stimulus (parameters: 2–4, 7, 12–13, 15–18, **Table 1**) were built using two PCAs (one per type of stimulus). Only the first principal component was kept in each PCA (HproxPC1 and OproxPC1) to be used as behavioral proximity score for a specific stimulus (variable loadings

TABLE 3 | Variable loadings of the behavioral parameters used in the Principal Component Analysis in the Isolation/Reunion test.

	Percentage per axis			**Relative cumulative values**		
	IsoReuPC1	**IsoReuPC2**	**IsoReuPC3**	**IsoReuPC1**	**IsoReuPC2**	**IsoReuPC3**
Cumulative inertia	31.5	70.5	82	–	–	–
Time spent standing immobile	22.89	3.49	6.33	−50.52	−5.20	−7.82
Time spent looking at exit door	2.98	37.10	13.93	−6.57	−55.32	−17.21
Time spent in proximal zone	6.69	5.34	47.46	14.77	7.96	−58.61
Time spent in distal zone	27.34	2.16	3.26	−60.33	3.22	4.03
Number of virtual zone changes	21.90	5.86	19.76	−48.32	8.74	−24.39
Time spent exploring the room	12.00	25.83	2.60	−26.47	38.52	3.21
Latency to enter proximal zone	6.21	20.22	6.66	−13.69	−30.15	8.22

All Principal components (PCs) having an Eigen value above one were kept to build behavioral response scores. The first line of the table indicates the cumulative inertia explained by the PCs. For each PC, the percentage of (left side) as well as the relative cumulative value (right side) of a given parameter is indicated. Parameters having a percentage above the uniform distribution can be considered as explanatory parameters for a given PC. Parameters quantifying total duration or numbers were standardized per minute.

Table 6). Only scores from day 1 were used, to minimize habituation effects that could occur on day two. For the human, HproxPC1 explained 63% of data variability and, for the object, OproxPC1 explained 47%. For further analyses, the score toward each stimulus was matched accordingly to the type of reunion the pig was experiencing (Human vs. Object): when reunited with the human, the behavioral proximity score toward the human (HproxPC1) was used, whereas when reunited with the object, the behavioral proximity scores toward the object (OproxPC1) was used.

Model selection: searching for the best predictors of vocal expression

During the reunion with a stimulus (Human or Object), several variables could explain the vocal expression of pigs: the day of the test (3 levels), the time during the test (index of the time interval in a zone as a continuous variable), the spatial proximity of the pig toward the stimulus (two levels: close to or away from the stimulus), the behavioral proximity of the pig toward the stimulus (continuous behavioral proximity score) or interactions between the type of stimulus and the location, between the type of stimulus and the behavioral proximity toward the stimulus or between the type of stimulus and the time during the test. To search for the best predictors of vocal expression, five acoustic variables were used as response variables. Three variables were linear: the acoustic spectral score PCac., the duration of grunt [log(grunt duration)] and the grunt rate (number of grunts per second, calculated when the number of grunts per interval was above three (186 intervals out of 286 intervals). Two non-linear variables were used: the total number of grunts (Poisson distribution), the number of times grunts were produced in series (Binomial distribution), i.e., when more than one grunt was produced in a given interval. Indeed, since we used only intervals containing at least three grunts to calculate the grunt rate, we needed to ensure we were not missing information on intervals containing fewer grunts, so we used the occurrence of one-grunt intervals to counteract the effect of interval selection.

A full model, describing the experimental design, was built as follows ("lmer" or "glmer" function of "lme4" R package): *Model 4 = Response variable ∼ day + stimulus + location + Z interval index + Z behavioral proximity score + stimulus*location + stimulus*Z behavioral proximity score + stimulus*Z interval index + location*Z behavioral proximity score +(1|individual)*. To increase interpretability, all continuous variables (interval index and behavioral proximity scores) were scaled, so the Z score is presented every time (32), the individual was put as a random factor to take into account multiple tests on the same pig. On this full model, a model selection was performed with the "dredge" function of the "MuMIn" R package (33), which compares all possible models built using subsets of the initial explanatory variables of the full model, including the null model. Models were compared using Akaike Information Criteria corrected for small sample size (AICc). Significant models were selected when delta AICc was below two (34), the weight of remaining explanatory variables was evaluated by calculating the presence or absence of the term in the remaining models ("importance" function). It should be noted that for the occurrence of one grunt intervals (Binomial model), no significant models were selected since the null model was contained in the best selected models (AICc<2). Although not mentioned in the results section, the model selection table is available (**Supplementary Table 7**).

Tests and Validation of All Models and Model Selection

All linear models were validated by visual inspection of the symmetrical and normal distribution of the residuals ["plotresid" in "RVAideMemoire" R package (35)]. For generalized models, overdispersion was tested using the "overdisp.glmer" function ("RVAideMemoire" R package); when overdispersed, a correction with the line number as random factor was used.

Anovas were computed on models to test for significant effects of explanatory variables ("car" R package), effects were considered significant when the *p*-value was below 0.05. Model estimates and pairwise *post hoc* tests were computed using Tukey correction for multiple testing ["lsmeans" R package (36) (models 1–3)]. A complete report of statistics is available as **Supplementary Tables 4–6**.

For the model selection (model 4), the analysis does not give *p*-values but rather a subset of significant models and weight of predictors. A model averaging step ("model.avg" function) gives the estimates of each of the predictors. The best predictors were the ones with a weight of one, meaning they were consistently present in all selected models. A complete report of all best equivalent models is available in **Supplementary Table 7**.

RESULTS

Choice Test Between Human and Object

The PCA allowed us to extract three behavioral response scores, respectively, choicePC1, choicePC2, and choicePC3 that explained cumulatively 81% of data variability (**Table 2**). Only the statistical analyses on PCs are presented in the result section, but **Supplementary Table 2** describes each behavioral parameter depending on the experimental conditions.

On the first behavioral response score (choicePC1, 45.8%), the mean duration in the stimulus zone, the proportion of time spent in the stimulus zone, the time spent in contact with the stimulus and the total time spent in the zone loaded negatively. Statistics revealed a significant effect of the interaction between the type of stimulus and the day of the test ($\chi^2_1 = 6.3$, $p = 0.012$), but *post hoc* tests did not show any difference between groups (pairwise tests with Tukey correction, $|\text{t.ratio}| < 2.2$, $p > 0.15$, **Figure 2A**). On the second behavioral response score (choicePC2, 19.5%), the number of visits in the stimulus zone loaded positively. Statistics showed no interaction between the type of stimulus and the day of the test ($\chi^2_1 = 0.7$, $p = 0.4$), a trend for an effect of the day ($\chi^2_1 = 3.3$, $p = 0.07$) and a main effect of the type of stimulus: PC2 was higher when considering the human zone compared to the object zone ($\chi^2_1 = 7.3$, $p = 0.007$, **Figure 2B**). On the third behavioral response score (choicePC3, 16%), the time the pig spent exploring the stimulus zone and the latency to approach the stimulus zone loaded negatively. Statistics showed no effect of explanatory variables on choicePC3 (Stimulus: $\chi^2_1 = 1.5$, $p = 0.2$, Day: $\chi^2_1 = 0.6$, $p = 0.5$). We examined the number of times

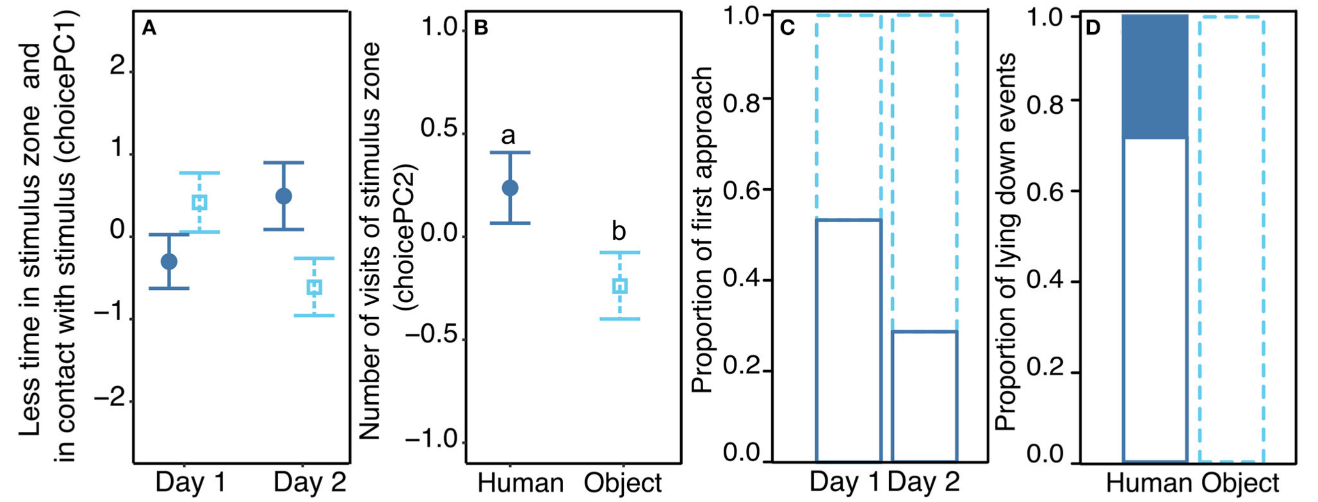

FIGURE 2 | Behavioral response in the Choice test. Mean (±se) of the two behavioral response scores from the PCA analysis, choicePC1 **(A)** and choicePC2 **(B)**, toward the two possible stimuli: either Human (filled dark blue circles) or Object (empty light blue squares). **(A)** Significant interaction between the stimulus and the day of the test but no differences revealed between groups in *post hoc* tests. **(B)** Significant effect of the stimulus on choicePC2. **(C)** first approach of the pig toward one of the stimuli either human (solid dark blue bars) or object (dotted light blue bars), indicated as proportion of the 24 pigs tested twice (day 1 and day 2). **(D)** Proportion of times that pigs laid down during the test either in the human zone or in the object zone. Different letters indicate significantly different groups ($p < 0.05$). All model estimates, anova tables, and results of *post hoc* tests are available in **Supplementary Tables 4–6**. Description of each behavioral parameter depending on experimental conditions is available in **Supplementary Table 1**.

the human zone or the object zone was first approached by the pig during the test. Statistics on this binary variable showed a trend for an effect of the day of the test: pigs tended to first approach the object zone more often on the second day than on the first day of the test ($\chi^2_1 = 3.4$, $p = 0.06$, **Figure 2C**). Finally, we counted the number of times pigs laid down near a stimulus zone; a χ^2 test showed a significantly different distribution of occurrences of this behavior, which only occurred in the human zone (by nine individuals out of 24) and never in the object zone ($\chi^2_1 = 12.8$, $p < 0.001$, **Figure 2D**). The position of the human in the room (left or right side) was included in all models and never showed a significant effect (see **Supplementary Table 4** for full report).

Isolation/Reunion Test

Variation in Pigs' Behavior When They Are Reunited With a Human or An Object

For the Isolation/Reunion test, a PCA allowed us to extract three behavioral response scores, respectively IsoReuPC1, IsoReuPC2 and IsoReuPC3 that explained cumulatively 82% of data variability (**Table 3**). Only the statistical analyses on PCs are presented in the results section, but **Supplementary Table 2** describes each behavioral parameter depending on the experimental conditions.

On the first behavioral response score (IsoReuPC1, 31.5%), the time spent immobile, the time spent in the distal zone and the number of changes of virtual zone negatively loaded. Statistics revealed a significant interaction between the type of reunion and the phase of the test ($\chi^2_2 = 16.6$, $p < 0.001$, **Figure 3A**). During the isolation phase, no significant difference was found between groups (pairwise comparisons human/object/no stimulus, $|\text{t.ratio}| < 0.7$, $p > 0.9$), whereas during the reunion phase the three type of reunion differed significantly in PC1 values (human vs. object: t.ratio $= 3.1$, $p = 0.03$, human vs. no stimulus: t.ratio $= 6.3$, $p < 0.001$, object vs. no stimulus: t.ratio $= 3.3$, $p = 0.02$). Furthermore, the reaction to each reunion type did not have the same magnitude. When pigs were not reunited with a stimulus, statistics did not show differences between the isolation and the reunion phases (isolation vs. reunion without stimulus: t.ratio $= 0.6$, $p > 0.9$), whereas when reunited with a stimulus, IsoReuPC1 showed a significant increase that was stronger with the human (isolation vs. reunion, t.ratio $= -6.3$, $p < 0.001$) than with the object (isolation vs. reunion, t.ratio $= -3.2$, $p < 0.03$).

On the second behavioral response score (IsoReuPC2, 39%), the time spent exploring the room loaded positively and the time spent looking at the entrance door and the latency to enter the proximal zone of the stimulus loaded negatively. A significant interaction was found between the type of reunion and the phase of the test ($\chi^2_2 = 41.5$, $p < 0.0001$, **Figure 3B**). During the isolation phase, no significant difference was found between groups (pairwise comparison human/object/no stimulus, $|\text{t.ratio}| < 2.7$, $p > 0.08$), whereas during the reunion phase the two types of stimuli differed significantly (human vs. object: t.ratio $= 4.9$, $p < 0.001$), as well as the reunion with the human compared to no stimulus (t.ratio $= 6.8$, $p < 0.001$), but no difference was found when comparing reunions with the object or without stimulus (t.ratio $= 2.0$, $p = 0.37$). The reaction to the three types of reunions also differed: from isolation to reunion phase, no

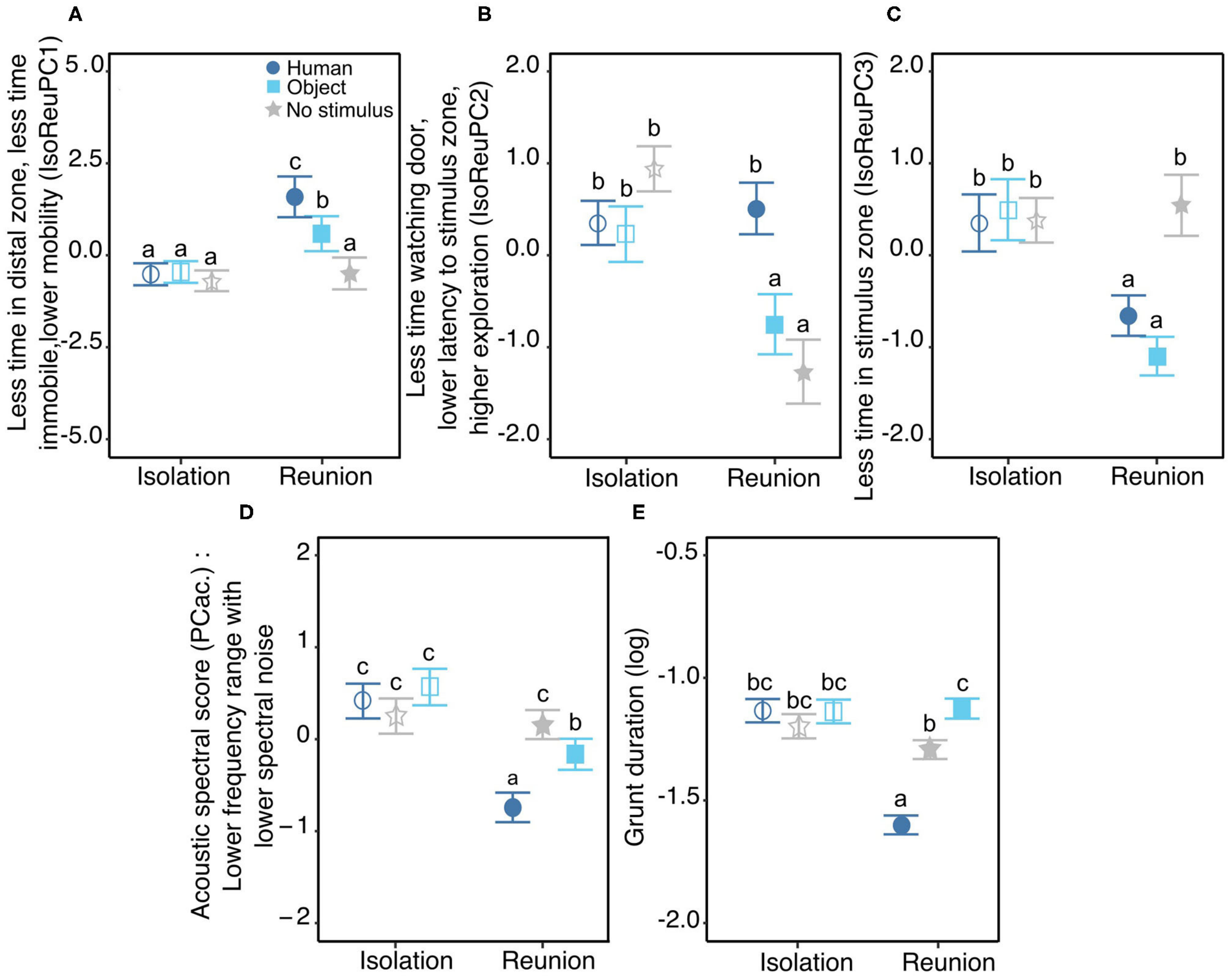

FIGURE 3 | Behavioral **(A–C)** and vocal **(D,E)** responses to the Isolation/Reunion test. Mean (±se) of behavioral and acoustic scores, according to the stimulus (Human = dark blue circles, Object = light blue squares, No stimulus = gray stars), the phase of the test (Isolation = empty symbols or Reunion = filled symbols) and/or the day of the test (day 1, 2, or 3). **(A–C)** significant interaction between the type of reunion and the phase of the test for the three behavioral response scores IsoReuPC1, IsoReuPC2, IsoReuPC3, respectively. **(D,E)** significant interaction between the type of reunion and the phase of the test for the two acoustic scores: the acoustic spectral score **(D)** and the logarithm of grunt duration **(E)**. Different letters show significantly different groups ($p < 0.05$). All model estimates, anova tables, and results of *post hoc* tests are available in **Supplementary Tables 4–6**. Description of each behavioral and each acoustic parameter depending on experimental conditions is available in **Supplementary Tables 2, 3**, respectively.

difference was found in IsoReuPC2 when pigs were reunited with the human (t.ratio $= -0.6$, $p = 0.9$), whereas PC2 decreased significantly when pigs were reunited with the object or without stimulus (object: t.ratio $= 3.8$, $p = 0.003$, no stimulus: t.ratio $= 8.5$, $p < 0.001$).

On the third behavioral response score (IsoReuPC3, 11.5%), the time spent in the stimulus zone loaded negatively. Statistics showed a significant interaction between the type of reunion and the phase of the test on IsoReuPC3 ($\chi^2_2 = 36.4$, $p < 0.001$, **Figure 3C**). During the isolation phase, no significant difference was found between groups (pairwise comparison human/object/no stimulus, $|\text{t.ratio}| < 0.7$, $p > 0.9$). During the reunion phase, IsoReuPC3 differed significantly for pigs being reunited without stimulus compared to being reunited with a stimulus (human vs. no stimulus: t.ratio $= -5.7$, $p < 0.001$, object vs. no stimulus: t.ratio $= -7.8$, $p < 0.001$), but IsoReuPC3 did not differ between the two types of stimuli (human vs. object: t.ratio $= 2.1$, $p = 0.3$). The reaction to the three types of reunions also differed: from isolation to reunion phase, no difference was found in IsoReuPC3 when pigs were not reunited with a stimulus (reunion with no stimulus: t.ratio $= -0.8$, $p = 0.9$), whereas IsoReuPC3 decreased significantly when pigs were reunited with the object or with the human (object: t.ratio $= 7.6$, $p < 0.001$, human: t.ratio $= 4.8$, $p < 0.001$).

The day of the test did not show any effect on IsoReuPC2 and IsoReuPC3 ($\chi^2_2 = 0.9, p = 0.6$, $\chi^2_2 = 0.2, p = 0.9$, respectively) but

TABLE 4 | Variable loadings of the parameters used in the Principal Component Analysis to build a spectral acoustic score.

	Acoustic spectral score (PCac.)	
	Percentage on axis	Relative cumulative values
Cumulative inertia	83.496	–
Mean	14.820	−98.992
Centroid	14.820	−98.992
Inter Quartile Range	13.624	−91.003
Spectral Flatness (sfm)	14.492	−96.802
Shannon index (sh)	14.398	−96.172
Entropy	13.797	−92.159
Mean Dominant frequency	1.193	−7.967
Spectral Standard Deviation (sd)	12.858	−85.885

All Principal components (PCs) having an Eigen value above one were kept to build an acoustic spectral response score. The first line of the table indicates the cumulative inertia explained by the PCs. Only one PC was kept. The table indicates the percentage of (left side) as well as the relative cumulative value (right side) of a given parameter. Parameters having a percentage above the uniform distribution can be considered as explanatory parameters for a given PC.

was significantly higher for IsoReuPC1 from day 1 to day 3 ($\chi^2_2 = 10.1$, $p = 0.007$, **Supplementary Figure 1A**). *Post hoc* testing showed the differences in IsoReuPC1 were progressive over days (pairwise comparison, day 1 vs. day2: t.ratio = −2.4, $p = 0.05$, day 1 vs. day 3: t.ratio = −3.0, $p = 0.009$, day 2 vs. day3: t.ratio = −0.6, $p = 0.79$).

Pigs' Grunt Acoustic Features When They Are Reunited With a Human, An Object Or Without Stimulus'

All 5,766 grunts produced during the test were analyzed using two acoustic scores: the logarithm of grunt duration and a spectral score. This spectral score is the first principal component of a PCA containing frequency and noise parameters of the calls (acoustic spectral score PCac., variable loading **Table 4**): the greater the score, the lower the frequency and the lower the spectral noise in the grunt. Only the statistical analyses on scores (temporal and spectral) are presented in the results section, but **Table 5** and **Supplementary Table 3** describe each acoustic parameter depending on the experimental conditions.

Concerning the spectral acoustic score (PCac.), a significant interaction was found between the type of reunion and the phase of the test ($\chi^2_1 = 45.1$, $p < 0.001$, **Figure 3D**). During the isolation phase, no difference was found between groups (pairwise comparison during isolation, human/object/no stimulus: $|\text{t.ratio}| < 1.9$, $p > 0.4$), whereas during the reunion phase significant differences were found between groups (pairwise comparisons during reunion, human vs. object: t.ratio = −4.9, $p < 0.001$, human vs. no stimulus: t.ratio = −9.2, $p < 0.001$, no stimulus vs. object: t.ratio = 3.7, $p = 0.003$). Furthermore, the reaction to each of the reunion types did not have the same magnitude of change. When pigs were subjected to another isolation, statistics did not show differences between the isolation and the reunion phase (t.ratio = 0.03, $p = 1$), whereas when reunited with a stimulus PCac. showed a significant decrease that was stronger with the human (t.ratio = 9.3, $p < 0.001$) than with the object (t.ratio = 5.3, $p < 0.001$). Statistics also showed a significant interaction between the type of reunion and the day of the test ($\chi^2_1 = 26.8$, $p < 0.001$) but *post hoc* tests revealed no significant pairwise comparisons ($|\text{t.ratio}| < 1.6$, $p > 0.8$, see **Supplementary Tables 4–6** and **Supplementary Figure 1B**).

Grunt duration showed a significant interaction between the type of reunion and the phase of the test ($\chi^2_2 = 210.1$, $p < 0.001$, **Figure 3E**). During the isolation phase, no difference was found between groups (pairwise comparison during isolation, human/object/no stimulus: $|\text{t.ratio}| < 2.6$, $p > 0.09$), whereas during the reunion phase significant differences were found between groups (pairwise comparisons during reunion, human vs. object: t.ratio = −19.5, $p < 0.001$, human vs. no stimulus: t.ratio = −16.7, $p < 0.001$, no stimulus vs. object: t.ratio = −3.9, $p = 0.003$). The reaction to each of the reunion types also differed. When pigs were subjected to another isolation or reunited with the object, statistics did not show differences between the isolation and the reunion phase (pairwise comparisons isolation vs. reunion object/ no stimulus: $|\text{t.ratio}| < 0.6$, $p > 0.6$), whereas when reunited with the human, grunt duration decreased significantly (pairwise comparison isolation vs. reunion, human: t.ratio = 9.3, $p < 0.001$). Finally, statistics also revealed a significant main effect of the day of the test ($\chi^2_2 = 20.0$, $p < 0.001$): grunt duration decreased as the day of the test increased, especially between the first 2 days (pairwise comparisons, day 1 vs. day 2: t.ratio = 3.9, $p < 0.001$, day 1 vs. day 3: t.ratio = 2.6, $p = 0.03$, day 2 vs. day 3: t.ratio = −1.2, $p = 0.4$, **Supplementary Figure 1C**).

Effect of Proximity to Stimulus on Vocal Expression

The following four acoustic variables: total number of grunts, grunt rate, duration of grunts [log(grunt duration)] and spectral acoustic score (PCac.) may be predicted by the context (the type of stimulus), the spatial proximity to the stimulus (location in the room), variables independent from the stimuli (day, time during the test, described by the interval index) or the experience pigs previously had with the stimuli. To quantify the experience pigs had with each stimulus (closeness and exploration), behavioral proximity scores resulting two from principal component analyses were built (**Table 6**) and one was selected per type of reunion: "behavioral proximity score" corresponded to the opposite sign of HproxPC1/OproxPC1 (respectively, for reunion with the human or the object) and was positively correlated with the time spent in contact with and near the stimulus. After model comparison and selection of the best equivalent models, the weight of predictors as well as the estimates of the averaged resulting model were calculated (**Tables 7**, **8**, respectively, full selected models in **Supplementary Table 7**).

The model selection showed the total number of grunts was predicted by the interactions between the type of stimulus and

TABLE 5 | Raw values for acoustic parameters used in acoustic scores for significant interaction groups (stimulus and phase of test interaction).

			Mean (Hz)		**Centroid (Hz)**		**Mean Dominant Frequency (KHz)**	
Stimulus	**Phase of Test**	**N**	**Mean**	**sd**	**Mean**	**sd**	**Mean**	**sd**
Human	Isolation	673	975.6	240.9	975.6	240.9	0.295	0.026
Human	Reunion	1,302	1135.0	240.9	1135.0	357.4	0.307	0.065
No stimulus	Isolation	775	1002.8	240.9	1002.8	280.9	0.295	0.037
No stimulus	Reunion	1,286	1018.4	240.9	1018.4	307.5	0.301	0.039
Object	Isolation	755	973.9	240.9	973.9	294.1	0.293	0.040
Object	Reunion	975	1042.7	240.9	1042.7	292.9	0.299	0.040
			Inter Quartile Range (Hz)		**spectrum standard deviation**		**Call duration (s)**	
Human	Isolation	673	636.4	504.0	1473.8	254.9	0.379	0.222
Human	Reunion	1302	941.1	768.4	1603.7	296.6	0.251	0.185
No stimulus	Isolation	775	719.7	617.1	1490.4	274.3	0.362	0.219
No stimulus	Reunion	1286	749.9	675.9	1493.4	281.7	0.333	0.207
Object	Isolation	755	650.3	623.3	1461.8	274.9	0.385	0.241
Object	Reunion	975	776.6	633.9	1524.8	266.5	0.385	0.222
			Shannon entropy		**Spectral Flatness**		**Entropy**	
Human	Isolation	673	0.651	0.067	0.270	0.087	0.501	0.049
Human	Reunion	1,302	0.686	0.079	0.319	0.114	0.517	0.058
No stimulus	Isolation	775	0.655	0.072	0.277	0.098	0.504	0.053
No stimulus	Reunion	1,286	0.660	0.077	0.280	0.104	0.506	0.058
Object	Isolation	755	0.647	0.074	0.267	0.100	0.498	0.054
Object	Reunion	975	0.669	0.074	0.291	0.098	0.516	0.054

The number of vocalizations per group and the mean and standard deviation (sd) are indicated. A more complete table is available in the ***Supplementary Table 3****. No statistics were run on these parameters (see Methods section).*

the location of the pig in the room, as well as the interaction between the type of stimulus and the behavioral proximity score (**Table 6**). Thus, a lower number of grunts was likely to occur when the pig was reunited with the object, and spatially close to it (**Figure 4B**). In addition, when reunited with the object, the higher the behavioral proximity score (-OproxPC1), the higher the probability of producing more grunts (**Figure 4A**), but this was not the case with the human. Concerning grunt rate, the type of stimulus was the only consistent predictor (**Table 7**): the rate of grunt was higher when pigs were reunited with the human, than with the object (**Figure 4C**).

Considering the acoustic structure of grunts (duration and spectral acoustic score PCac.), both descriptors were best predicted by the interaction between the location in the room and the type of stimulus, the behavioral proximity score, the interval index and the day (**Table 7**). The probability of having shorter grunts was higher when reunited with the human and close to her (**Figure 4D**). In addition, the higher the behavioral proximity score, the higher the probability of having shorter grunts (**Figure 4E**). The probability of having longer grunts increased as the time of the test increased (interval index, **Figure 4F**) with no interaction with the type of stimulus or location. Finally, as the day of the test increased, the probability of having shorter grunts increased (slope estimate ± se: -0.13 ± 0.04 and -0.04 ± 0.04, respectively, for day 2 and 3, **Table 8**), with no interaction with the type of stimulus. Concerning the acoustic spectral score (**Figure 4E** and **Table 8**): the probability of producing grunts with a lower acoustic spectral score depended of the type of stimulus and the spatial proximity, as the acoustic spectral score was more likely to decrease when approaching the object but not the human (**Figure 4G**).The higher the behavioral proximity score, the higher the probability of producing grunts with a lower acoustic spectral score, independently from the type of stimulus and location in the room (**Figure 4H** and **Table 8**). As the time during the test increased, the probability of producing grunts with a higher acoustic spectral score increased, independently from the type of stimulus or location (**Figure 4I**). Finally, as the day of the test increased, the probability of producing grunts with a lower acoustic spectral score increased independently of the type of stimulus (slope estimate ± se: -067 ± 0.26 and -0.51 ± 0.27, respectively, for day 2 and three, **Table 8**).

DISCUSSION

No Evidence of a Preference Toward a Stimulus But Specific Human Directed Behaviors

In a V shaped arena Choice test, comparing the time spent close to and in contact with each stimulus (first behavioral

TABLE 6 | Variable loading of PCA describing pig-stimulus behavioral proximity.

	Human proximity score (HproxPC1)	Object proximity score (OproxPC1)
	Percentage on axis	
Cumulative inertia (%)	63.075	46.988
Latency to approach stimulus zone	1.304	0.031
Number of times in stimulus zone	1.859	0.204
Mean duration in stimulus zone	13.311	26.097
Total time in stimulus zone	18.363	31.575
Total time all contacts (human)	16.822	–
Total number of all contacts (human)	16.191	–
Total time of initiated contacts toward stimulus	15.834	30.142
Total number of initiated contacts toward stimulus	16.318	11.951
	Relative cumulative values	
Latency to approach stimulus zone	6.578	0.087
Number of times in stimulus zone	−9.378	−0.575
Mean duration in stimulus zone	−67.165	−73.574
Total time in stimulus zone	−92.657	−89.020
Total time all contacts	−84.882	–
Total number of all contacts	−81.699	–
Total time of initiated contacts toward stimulus	−79.899	−84.978
Total number of initiated contacts toward stimulus	−82.342	−33.693

Only the first Principal component was kept to create a score to be used as an explanatory continuous variable. The first line of the table indicates the cumulative inertia explained by the selected PC, the percentage of (above) as well as the relative cumulative value (below) of a given parameter is indicated. Parameters having a percentage above the uniform distribution can be considered as explanatory parameters for the PC. Behavioral parameters used to build these scores were extracted from the first Choice test. For statistics, the behavioral proximity score toward each stimulus was matched according to the type of reunion the pig was experiencing (Human vs. Object): when reunited with the human, the behavioral proximity score toward the human (HproxPC1) was used, whereas when reunited with the object, the behavioral proximity score toward the object (OproxPC1) was used.

response score, choicePC1), or the latency to reach the stimulus zone and exploring the stimulus zone (third behavioral response score, choicePC3), did not lead to significant differences between the types of stimuli. Neither was evidence for a consistent choice found when considering the first approach. Therefore, no consistent conclusion on a preference toward one of the stimuli can be drawn. Using the home pen to test for preference, as in mice for instance (37), may have led to different results, although the technical procedures would have been much more complicated. Indeed, male mice may show preferential attraction to different enrichment stimuli in such a situation (38). However, no particular negative behaviors associated with fear or stress were recorded during the test, thus the situation itself may not have been negative for our pigs. In addition, the absolute time spent close to each of the stimuli (between 73.9 and 100 s out of 300 s) or in contact with the stimulus (between 28.5 and 67.8 s out of 300 s, **Supplementary Table 5**) were high enough to conclude that the stimuli were attractive. In addition, two differences were apparent between the human and the object. The pigs more often entered the human zone than the object zone (second behavioral response score, choicePC2) and the number of times pigs laid down near the stimulus was human zone specific. Lying down is a sign of absence of stress in pigs (39), and the location was not by chance here. We may hypothesize that the human had reassuring effects, as has been found in studies on other farm animal species (19, 20). This would need to be confirmed, for example by using other non-invasive ways allowing positive emotional state to be monitored, such as heart rate and its variability. The novel structure of the testing pen compared to that experienced previously by the pigs (open pen) may have attracted their attention more than the familiar stimuli present in the pen.

Behavioral Evidence for Positive Attractiveness of Both a Manipulable Object and a Familiar Human

Isolation/reunion tests allowed us to show differential responses according to the stimulus pigs were reunited with. Behavioral measures showed that both stimuli were attractive for the

TABLE 7 | Weight of predictors for each response variable.

	N	Stim	Day	Loc	-Behav Prox	Stim *Day	Stim *Loc	Stim *-Behav Prox	Loc *-Behav Prox	Int Index	Stim *Int index
Total Number of grunt-*Poisson*	2	1.00	1.00	1.00	1.00	–	1.00	1.00	0.47	NA	NA
Grunt rate (log)	2	1.00	–	–	0.30	–	–		–	–	–
Grunt duration (log)	6	1.00	1.00	1.00	1.00	–	1.00	0.24	0.25	1.00	0.51
Acoustic spectral score (PC1ac.)	9	1.00	1.00	1.00	1.00	0.36	1.00	0.44	0.13	1.00	0.24

The number of equivalent best models (N), and each term of the full initial model are indicated in columns: “Stim” for stimulus type, Day, “Loc” for location in the room (Close to or Away from the stimulus), “Int. Index” for interval index, “Behav Prox” for behavioral proximity score, as well as relevant interactions between explanatory variables. Only weights different from zero are indicated. For the total number of grunts, since the variable is a sum of all intervals per day, location, individuals and type of stimulus, the interval index was not included in the full model and referred as “NA.” The best predictors are the one consistently appearing in all equivalent selected models so the ones having a weight of “1”.

TABLE 8 | Estimates (standard error) of terms contained in the equivalent best selected models.

	(Intercept)	**Stim. (Object)**	**Day (2)**	**Day (3)**	**Loc. (Close)**
Total Number of grunt *(Poisson)*	2.770 (0.166)	0.048 (0.074)	0.202 (0.068)	0.010 (0.072)	0.064 (0.060)
Grunt rate (log)	−1.563 (0.133)	−0.428 (0.092)	–	–	–
Grunt duration (log)	−1.496 (0.075)	0.390 (0.042)	−0.125 (0.041)	−0.035 (0.044)	−0.272 (0.039)
Acoustic spectral score (PC1)	−0.222 (0.262)	0.503 (0.276)	−0.660 (0.261)	−0.506 (0.274)	0.191 (0.165)

	Int. Index	**-Behav Prox**	**Stim. (object) * Loc. (Close)**	**Day (2) * Stim. (Object)**	**Day (3) * Stim. (Object)**
Total Number of grunt *(Poisson)*	NA	0.053 (0.055)	−0.501 (0.098)	–	–
Grunt rate (log)	–	0.021 (0.031)	–	–	–
Grunt duration (log)	0.108 (0.018)	−0.056 (0.026)	0.223 (0.060)	–	–
Acoustic spectral score (PC1)	0.285 (0.074)	−0.225 (0.109)	−0.644 (0.255)		

	Stim. (object) * Int. Index	**Stim. (object) * –Behav Prox**	**Loc. (Close) * –Behav Prox**
Total Number of grunt *(Poisson)*	NA	0.466 (0.101)	−0.038 (0.025)
Grunt rate (log)	–	–	–
Grunt duration (log)	−0.027 (0.019)	0.014 (0.020)	0.007 (0.009)
Acoustic spectral score (PC1)	−0.041 (0.053)	−0.143 (0.106)	−0.009 (0.027)

When the term is a factor, the estimate is indicated for one level and the absolute value has to be calculated using the estimate of the intercept, the level compared is indicated. When the term is a continuous covariate, the estimate of the slope is indicated, notice that to increase interpretability, all continuous variables were scaled so the value is for the Z score. "–"the term was not selected in the best equivalent model. "NA" the term was not in the full model prior to the model selection.

pigs, with a decrease in the time spent in the zone distant from the stimulus and an increase in the time spent in the stimulus zone when pigs were reunited with the human or the object compared to remaining alone in the experimental room. Furthermore, pigs remained immobile for a shorter time during the test and they had a lower locomotor activity when a stimulus was present. Remaining immobile (without exploring or watching a specific part of the room) may be associated to an attentive state or vigilance. Therefore, these changes in locomotor activity may be explained along with the time spent near the stimulus and are in line with the hypothesis of attraction to the stimuli. Beyond these general changes in behavior, pigs expressed discriminatory behaviors according to the stimulus present. Indeed, in response to a reunion with the human compared to the object, pigs were quicker to enter the stimulus zone, expressed a lower mobility and a higher exploration time. In response to a reunion with the object, pigs spent more time watching the exit door than exploring the room, a response equivalent to the reunion phase without any stimulus (i.e., isolation). Therefore, results suggest that the presence of the familiar human may prevent the pigs from expressing stress responses (more vigilance behavior and less exploration), a hypothesis strengthened by the fact that being reunited with the object or without any stimulus seem equivalent in terms of postural and locomotory behaviors.

Acoustic Evidence of a High Arousal Positive Emotional State With the Human and a Low Arousal Negative Emotional State With the Object

We predicted that, if vocalizations reflect expression of the emotional state of the pigs, acoustic scores should be different when pigs are reunited with a stimulus compared to without one (isolated). In reaction to the reunion with the familiar human, the duration of grunts decreased and this was not the case with the object or when pigs remained alone. Shorter vocalizations have been associated with positive contexts compared to negative ones in many species (40), and especially shorter grunts in pigs (24, 28). We can compare the absolute values of grunt duration from the present study (250 ± 180 ms with human, 380 ± 220 ms with object, 330 ± 210 ms isolated, **Supplementary Table 3**) and other studies (negative vs. positive context (41): 480 ms vs. 280 ms; negative vs. positive context (24): ∼430 ms vs. ∼350 ms; anticipation of social reunions with pen mates (26): ∼240 ms. Although comparisons must be made with caution, due to the material and methodological specificity of each study, the range of values we obtained with the human are in the range of other positively perceived situations. Behavior and acoustics together may allow us to conclude that being reunited with the human leads to a more positive context than reunion with the object.

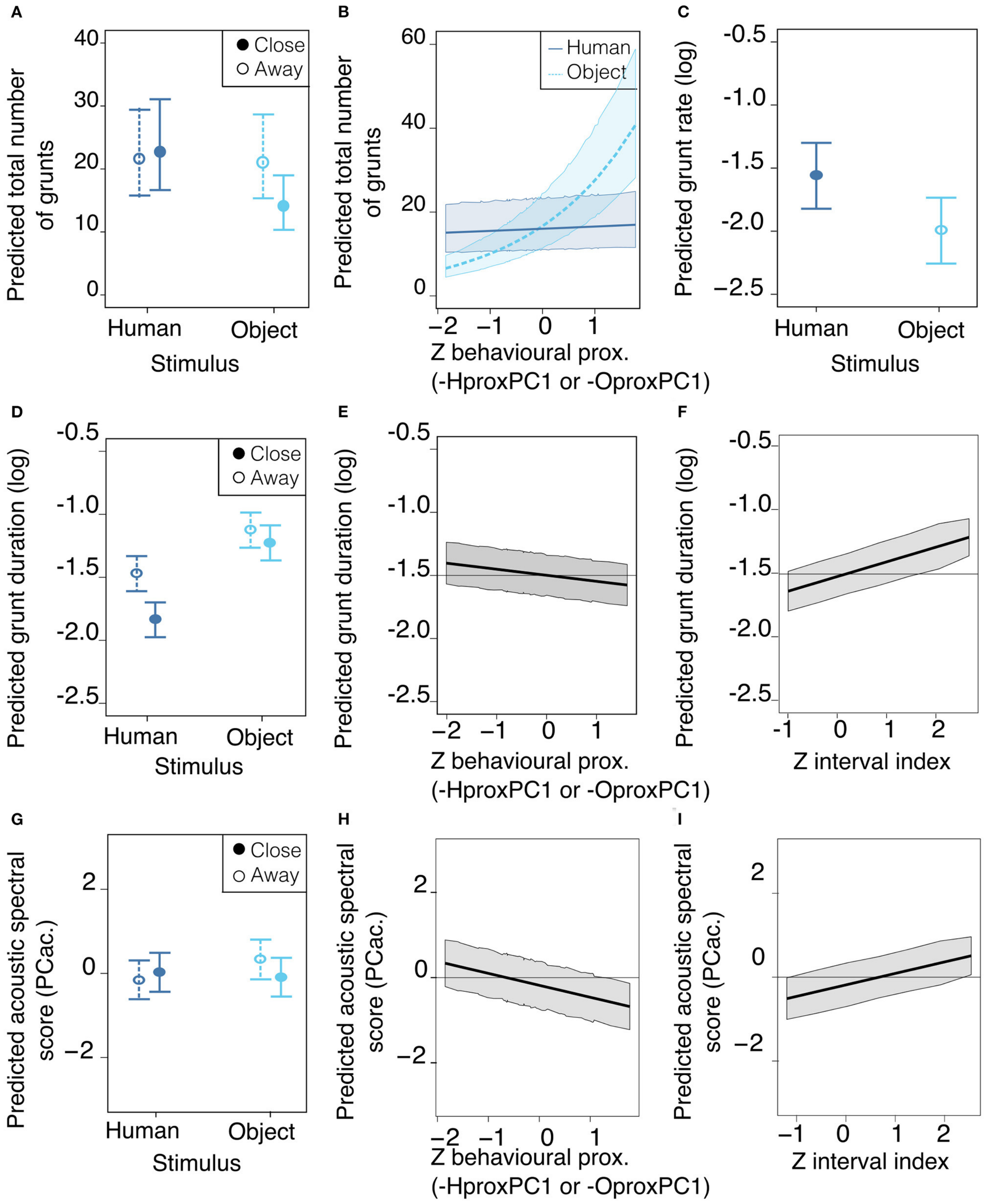

FIGURE 4 | Mean estimates and 95% confidence interval of best predictors of vocal expression: number of grunts **(A,B)**, grunt rate **(C)**, grunt duration **(D–F)** and acoustic spectral score PCac. **(G–I)**, depending on stimulus cyan for object, dark blue for human, location in the room, behavioral proximity and time during the test. Best predictors are represented for illustrating the range and directions of effects. Location **(A,D,G)**: whether the pig was located close to the stimulus (solid lines) or

(Continued)

FIGURE 4 | away from it (dotted lines). Behavioral proximity score **(B,E,H)** was scaled for the statistical analysis so the Z score is represented (see composition of scores in **Table 6**). **(A–D,G)** Type of stimulus: whether the reunion was with the human (dark blue solid circles and lines) or the object light blue empty circles and dotted lines. Time during the test **(F,I)** is quantified by the interval index during the test and is scaled, so the Z score is represented. Plots were generated using the averaged best model resulting from the model selection (models having delta AICc below 2 and predictors having a weight of 1), for which the estimates (se) are in **Table 8**, the full selection model table is available in **Supplementary Table 7**.

Since the human has previously been associated with positive tactile contacts, known to promote a positive state (14, 16), the presence of the human may engage the pigs in a positive anticipation of tactile interactions. Being reunited with the object appeared to lead to the expression of an emotional state not different from being without a stimulus (i.e., negative effect of isolation) even if it was attractive to some extent. Hence, behavioral and vocal clues do not seem to provide indications which point in the same direction. However, we can hypothesize that, even if the object is attractive, pigs may express frustration that they are not reunited with the human providing positive contacts. In addition, as shown by Villain et al. (26), even when two situations are behaviorally considered positive, pigs may rank the two situations and classify one of them as relatively negative. In fact, in Villain et al. (26), pigs vocally expressed the frustration of being reunited with the human and not their conspecifics. Here, a similar mechanism may be at play: pigs may express the frustration of being reunited with the inanimate object when they could have had positive contacts from a human instead.

During the reunion with either the object or the human, the spectral acoustic score of pig grunts decreased: grunts were composed of higher frequencies and a higher noise component, and this effect was greater with the human compared to the object. Changes in spectral components in response to changing contexts may be associated with the arousal of situations in mammals (26, 42). This may underline that the reunion with a stimulus promotes emotional states of high intensity in pigs, especially the reunion with a human. Villain et al. (26) showed that pigs were able to rapidly change the spectral properties of their grunts when anticipating positive events. The anticipation of a reunion with familiar conspecifics led to noisier grunts, whereas the anticipation of a reunion with a familiar human associated with positive contacts led to higher pitched grunts. In the present study, frequency and noise components of the grunt are closely intercorrelated, so it is not possible to discriminate between the two.

From the comparisons of grunt durations and spectral scores, we can summarize that being reunited with a familiar human at least alleviates the distress of isolation, but may also induce a high arousal and positive emotional state, through reassuring effects, while being reunited with a familiar object may induce a low arousal negative emotional state, after a social isolation. Thus, a positive relationship with a human seems to be more valuable as an enrichment for pigs. This may result from the relationship created through the numerous sessions of positive vocal and tactile interactions, as already shown in previous studies (16, 22). An inanimate object may not acquire similar properties. As a consequence, promoting social or pseudo-social enrichment in pigs is a good way to enhance their welfare.

Experience and Spatial Location Predict Differences in Spectro-Temporal Features of Grunts Depending on the Stimulus

To investigate further, we studied which variables predicted vocal characteristics. From the model selection, we found that the type of stimulus (object or human) was among the best predictors of vocal expression (number of grunts, grunt rate, duration, and spectral score) and was the only consistent predictor explaining the temporal dynamic (grunt rate). Being reunited with a human (but not an object) is associated with more vocal production and at a higher rate. Morton (43) explained that the rhythm of a behavior can be positively linked to motivation of the producer, and thus a higher arousal. Villain et al. (26) showed that pigs had a higher grunt rate when anticipating the arrival of conspecifics, compared to a familiar human. In the present study, we would interpret the result in the direction of a higher motivation toward the human compared to the object.

Being reunited with the human and being close to them is likely to induce shorter grunts, whereas being reunited with the object and close to it is likely to induce a lower number of higher frequency and noisier grunts. This is in line with the more positive state, through reassuring effects, induced by the familiar human compared to the object after a short period of social isolation.

The behavioral proximity score, associated with the number of interactions and the time spent in contact with or near the stimulus, was a consistent predictor for both acoustic scores. Independently from the type of stimulus, the higher the behavioral proximity to the stimulus, the higher was the probability of producing shorter grunts with higher frequencies and noise components. This raises the possibility to monitor the degree of behavioral proximity to an enrichment by analyzing the structure of grunts (28).

The time during the test was also a predictor of the spectro-temporal features: the later in the test, the higher was the probability of producing longer, lower pitched and less noisy grunts (effect of interval index) and this result was independent from the type of stimulus. We can hypothesize that the positive effect of stimulus presence may be attenuated with time during the test and/or that negative effects of isolation from penmates may increase. In addition, since during the test the human did not interact with the pig as she would have done outside of the test situation, we can hypothesize either that the test makes the human more like an inanimate object and pigs may habituate to the stimulus, or that pigs may be frustrated if the human does not interact with them as in Tallet et al. (16). It would be interesting to investigate whether interacting with the pig during an Isolation/Reunion test may prolong the positive effect of the reunion with a familiar human after a 5 min isolation. Finally, over successive days grunts were more likely to be shorter, higher pitched and noisier, independently from the type of stimulus. This may have been linked to habituation to the test protocol.

Is a Familiar Human More Than an Enrichment? Implications for Pig Welfare and Welfare Policies

Although paradigms generally used to quality an entity as "environmental enrichment" are usually performed in the home pen, our study shows similarities between what should be expected from an enrichment in the home pen and the responses we observed during the Isolation/Reunion test. Indeed, the reunion with a familiar object or human led to an attraction toward the stimulus and repeated contacts, as well as a decrease in attentive/vigilance behavior. These parameters are in line with the definition of what an enrichment should promote, that is to say a sustainable attraction and oral manipulations (5, 8). Therefore, it would be possible to extend the way we test for enrichment to other contexts than the home pen in future studies.

In addition, compared to an inanimate object, being with a human and/or close to the human provokes higher degrees of behavioral change in pigs (both spatial and vocal), and specific behavioral postures (lying down), associated with positive states. Regarding vocal behavior, although we showed that the behavioral proximity to the stimulus and vocal responses correlated, only the human presence led to positive shorter grunts during the reunion. Thus, analyzing vocal behavior enabled us to distinguish between the two kinds of stimuli and have insights into the emotional state of the pigs. This would imply that considering only postural/exploratory behaviors and describing attraction and contacts may not be enough to classify a stimulus as enrichment. We may need other non-invasive parameters such as vocalization monitoring, that do not entail a need to handle the animal.

With both postural/exploratory and vocal behaviors we conclude that, following a stressful isolation, only a familiar human and not an inanimate object is capable of generating a positive emotional state through reassuring properties. In a sense, human presence may be more than an enrichment and should be considered in further political decisions. Indeed, novelty is a paramount feature to promote a long term positive context and delay habituation effects (44). It is possible that interactions with the human may allow this feature, as a human is moving, talking and is unlikely to reproduce exactly the same gesture, at the same rhythm, which may contribute to promoting a higher level of stimulation than an object can provide. More studies are needed to better describe what are the most efficient human signals and behaviors that promote positive emotional states using a multimodal approach: voice? (45), shape? facial expression? [e.g. goats (46)], facial cues (47) or odors? [review in (48)], combinations of factors? (49).

CONCLUSION

Using behavioral monitoring, this study showed that a manipulable inanimate object and a familiar human can be attractive for weaned pigs away from their rearing environment. Vocal monitoring showed that only the familiar human, but not the inanimate object, may alleviate the stress following of social isolation and induce a positive and high arousal emotional state when the pig is reunited with a familiar human, through reassuring effects. More studies should consider pseudo-social interactions between humans and pigs to enhance welfare, through a better relationship between the pigs and the humans. In order to be applicable on a larger scale, we must better understand the timing for the establishment of an effective human-pig relationship, as well as the most efficient signals triggering positive emotional states in pigs.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://doi.org/10.15454/GDLDBH.

ETHICS STATEMENT

The animal study was reviewed and approved by Ministry of Higher Education, Research and Innovation, APAFIS#17071-2018101016045373_V3.

AUTHOR CONTRIBUTIONS

AV, CT, and ML conceived and designed the experiment. AV, CT, and ML contributed to the writing of the manuscript. AV, CG, and ML: performed the experiment and collected and edited the acoustic and behavioral data. AV did the statistical analyses. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2020.577433/full#supplementary-material

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Inside the Interaction: Contact With Familiar Humans Modulates Heart Rate Variability in Horses

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A human–animal relationship can be developed through subsequent interactions, affected by the positive or negative emotional valence of the proceeding one. Horses implement a process of categorization to classify humans with whom they interact as positive, negative, or neutral stimuli by evaluating the kind of approach and the nature of the contact. In these terms, human–animal interactions are emotionally charged events, eliciting specific emotional states in both subjects involved. Although the human–horse relationship has been mainly investigated through behavioral analysis, physiological indicators are needed for a more objective assessment of the emotional responses. Heart rate variability (HRV) is a commonly used autonomic nervous system (ANS) correlate estimating the sympathovagal balance as a psychophysiological marker of emotion regulation in horses. We have assumed that long-term positive relationships with humans may have a positive and immediate impact on the emotional arousal of the horse, detectable, *via* ANS activity, during the interaction. We analyzed horses' heartbeat dynamics during their interaction with either familiar or unfamiliar handlers, applying a standardized experimental protocol consisting of three different conditions shifting from the absence of interaction to physical contact. The ANS signals were monitored through an innovative non-invasive wearable system, not interfering with the unconscious emotional response of the animal. We demonstrated that horses appeared to feel more relaxed while physically interacting (e.g., grooming on the right side) with some familiar handlers compared to the same task performed by someone unfamiliar. The shift of the sympathovagal balance toward a vagal predominance suggests that the horses experienced a decrease in stress response as a function not only of the handler's familiarity but also of the type of interaction they are experiencing. These results constitute the objective evidence of horses' capacity to individually recognize a familiar person, adding the crucial role of familiarity with the handler as a paramount component of human–animal interaction. Our rigorous methodological approach may provide a significant contribution to various fields such as animal welfare while further investigating the emotional side of the human–animal relationships.

Keywords: *Equus caballus*, human–animal relationship, inter-specific interaction, heartbeat dynamics, autonomic nervous system, emotional valence

INTRODUCTION

Horses can discriminate between familiar and unfamiliar humans using both visual and vocal cues (1, 2); they are also able to form a long-lasting memory of a specific subject (3, 4). This ability suggests that the level of familiarity can affect horses' tendency to engage again with the same human (5), also allowing these animals to recognize their caretakers long after the last encounter (6).

Indeed, human companions have a greater chance of leaving a positive image in horses' memory if their behavior is appropriate starting from the first approach. This may occur during training procedures or stable management (7), which the animal may recall for several months (8). The human–animal relationship is built on a succession of basic interactions, and the "positive" or "negative" valence of each interaction determines the occurrence of the next one (9). Therefore, by evaluating attitudes, kinds of approach, temperament, and the nature of the last contact, horses are able to implement a "categorization" process in order to label humans as positive, negative, or neutral stimuli (10). The motivation to react to perceived stimuli has an adaptive value, eliciting approaching behaviors toward survival sources or triggering avoidance in those situations perceived as a threat. These motivational factors, affecting the probability to move toward or away from stimuli (approach/avoidance), are significantly correlated with the valence (i.e., pleasantness) and the arousal (i.e., perception intensity) of the stimulus, as the two main components of emotion perception (11). Any emotional event can be either positive or negative. These tags, embodying emotive valence, differ in how they arouse an individual (11, 12). Similarly, human–animal interactions can be considered emotionally charged events, the positive/negative valence of which determines the ultimate quality (13). Investigating the emotional side of the human–animal bond can provide stimulating insights into animal cognition and social behavior. Hence, emotions affect communication with others, which constitutes a building block of the evolution of social species. This approach has generated detailed studies on behavioral and physiological indicators of emotions [e.g., (14–16)]. In prey species such as horses, visible behavioral markers of fear or distress may run counter to their survival strategy (17, 18). Although behaviors provide an immediate way to determine the response of an animal to environmental factors, the accurate interpretation of behavioral signals needs to be corroborated by physiological indicators (19, 20). Emotions, in fact, are expressed through a set of coordinated responses, including physiological signals (21, 22), which are affected by the social interaction and may determine its outcomes. In the case of horses, for example, the nature of their interaction with humans, which may shift from occasional management to a more intimate bond in daily contact, is reflected in their physiological and emotional responses. The most used autonomic nervous system (ANS) correlations for behavioral assessment are heart rate and heart rate variability (HRV). Heart rate corresponds to the number of heart beats per unit of time, and these beats are slowed down or accelerated by parasympathetic activity or sympathetic activity, respectively. HRV describes normal fluctuations in the time intervals of consecutive heartbeats, thus reflecting the interplay between the sympathetic and parasympathetic nervous systems. In particular, HRV indicates the shift from an autonomic balance toward a sympathetic dominance, adding extra information about individual temperament and reactivity to stimuli (23). Changes in the ANS have been increasingly used as an indicator of stress level in many species as a way to further employ this approach to animal behavioral assessment. With regard to companion animals, such as horses, the sympathovagal balance as a psychophysiological marker of emotion can be estimated *via* HRV (24, 25). Scientific evidence indicates that a modification in the time interval between successive heartbeats may imply a neurophysiological response to stress (24–29). The current challenge is to find a way to define the human–horse relationship by measuring its multifaceted aspects, particularly on the level of familiarity connecting the participants and the emotional valence punctuating the whole experience. In the present study, we hypothesize that long-term positive relationships with humans may have a positive and immediate impact on the emotional arousal of the horse. We expect the ANS activity of the horse to reflect a relaxed psychophysiological state while it experiences a familiar human interaction. To verify this hypothesis, we analyzed the heartbeat dynamics of horses during their interactions with both familiar and unfamiliar handlers. To this aim, we selected familiar people from among those who are mainly involved in the horse's daily activities such as management or training. To represent unfamiliar humans, we recruited people who were already familiar with horses but were unknown to our test subjects. Standardized interaction tests between humans and horses were designed to understand how horses perceive physical closeness and being handled by a human.

MATERIALS AND METHODS

Ethical Statement

The study was performed in accordance with the ethical standards of the Declaration of Helsinki and with the recommendations of the Italian Animal Care Act (Decree Law 26/2014). The Ethical Committee on Animal Experimentation of the Experimental Zooprophylactic Institute of Venice (IZSVe) approved the experimental protocol in each of its parts (i.e., handling procedures, data collection methods, CE IZSVe 07/2020). Human subjects were enrolled on a voluntary basis, and they signed an informed consent statement to take part in the study. They were advised about their rights, data management, and protection in accordance with the Reg. EU N. 679/2016. The horses' owners gave written consent to the use of their horses in this experiment.

Animal Subjects

We selected 23 mixed-breed horses (mean 14 ± 6.98 SE years old, nine mares and 14 geldings) from three different stables, all located in Italy (see **Table 1** for details). All enrolled horses were in good health and showed no signs of injury. Exclusion criteria included the presence of any abnormal behaviors or stereotypes or the horse's involvement in any kind of professional equestrian sports. We chose participating stables based on management

TABLE 1 | Horses selected from three different stables.

Individual	Stable	Sex	Breed	Age
Ckendy	NPP	F	Haflinger	20
Dado	NPP	G	Sardinian anglo-arabian	12
Didol	NPP	G	Argentino	23
Friso	NPP	G	Friesian	8
Ivan	NPP	G	Belgian double pony	27
Neve	NPP	F	Camargue	21
Remy	NPP	G	Haflinger	14
Arabella	AE	F	Sella italiano	28
Arramon	AE	G	Haflinger	19
Betta	AE	F	Arabian	9
Danilù	AE	G	Sella italiano	10
Dragonhair	AE	G	Sella italiano	10
Ercole	AE	G	Friesian	13
Falco	AE	G	Maremmano	13
Oliver	AE	G	Haflinger	11
Saif	AE	G	Arabian	8
Sunny	AE	F	Hanoverian	21
Erika	RdC	F	Monterufoli	8
Ilex	RdC	G	Monterufoli	4
Gelso	RdC	G	Monterufoli	6
Ginepra	RdC	F	Monterufoli	6
Uga	RdC	F	Monterufoli	15
Ginestra	RdC	F	Monterufoli	6

NPP, Nero Per Passione; AE, Addestramento Etologico; RdC, Riserva di Cornocchia. F, female; G, gelding.

standards, including handling procedures and riding activities. In particular, we evaluated the primary activities undertaken by each horse, their daily workload, the number of people they were used to interacting with during activities and/or for management, their social life with conspecifics, and feeding management. Selected subjects were mostly involved in amateur-level riding activities with up to 3 h of ridden or ground work per day. The horses were accustomed to interactions with two to six people for daily management and to many more for the aforementioned activities. We accepted horses group-housed in paddocks, provided they spent short periods of time in a single stall as needed. This allowed us to exclude the possibility of inducing stress during the experimental tasks that could arise from being isolated in a box away from the social group. All subjects had free access to water. Pastures were supplemented with hay; some horses received concentrated feed and/or small amounts of vegetables.

Human Subjects

We recruited human volunteers from different equestrian establishments between May and September 2019, on a network basis of personal contacts who themselves recruited volunteers in their respective locations and from their horse-owning contacts. We enrolled 22 subjects overall (mean 35.36 ± 13.17 SE years old; 12 females, 10 males). Among them, 12 people participated in the study as familiar persons and 10 as unfamiliar ones. To each familiar person, an unfamiliar same-sex person was matched. None of the involved human participants had any background of psychiatric or psychological disorders. All handlers were required to have experience with and be confident in handling horses. The unfamiliar handlers were a convenience sample of people who were present at the location or, at the time of the study, were not familiar with the horse to be tested. All humans involved in the trials wore similar clothes (specifically, blue jeans and a blue long-sleeved shirt) during the tasks. Starting 1 week before the start of the experiment, they were all required to use the same odorless neutral pH products. This procedure helps exclude the bias of familiar body odors' recognition.

Protocol of Interaction

The experimental protocol, modified after (30, 31), consisted of an interaction task with three different conditions, each one lasting 5 min, combining a familiar/unfamiliar human handler test with the concomitant recording of horses' ECGs. The order of interactions with familiar/unfamiliar humans was randomized.

Session 1 (S1) – During the first phase, the human subject and the horse were left alone in separate areas. The horse was left free to move in its own familiar stall (4 × 4 m) (32), while the person was standing in the stable's service room. This session was considered the resting phase to collect basal ECG signals.

Session 2 (S2) – Successively, human subjects moved from the service room to the stall of the horse itself. They entered, without other humans, and placed themselves near the door and stood still, staring at the floor. In the meantime, the horse was still free to move and explore the environment. This phase implied both visual and olfactory interactions. In this session, the horse controlled interactions, deciding whether to approach, sniff, touch, or stay away from the human.

Session 3 (S3) – At the end of session 2, the human subject took a brush previously positioned outside the box, within arm's reach. He or she approached the horse to brush it. The grooming session lasted 2.5 min on each side (S3L left side and S3R right side) in a randomized order among the subjects. If the horse tried to move, the person had to maintain contact with it to keep on with the grooming procedure. Unlike the previous phase, this time the person had control over the interaction, constantly seeking connection with the animal. The horse could not avoid the interaction.

ECG Signal Collection

The ANS response plays an essential role in the study of the familiar vs. unfamiliar horse interplay; therefore, in the experimental phase, the ECGs of both humans and horses were monitored through two wearable systems (33, 34).

Comfort and strong adaptability to experimental conditions are just a few of the advantages the wearable systems showed. Moreover, the systems developed by the University of Pisa for both humans and animals guaranteed a suitable solution for ANS monitoring without interfering with the hidden and unconscious emotional responses arising from the human–horse interaction. The belt used for horses was specifically designed to not be more intrusive than a saddle or any similar riding equipment, and the functionality of the belt has been previously validated (35, 36). Particularly, the two textile-based monitoring systems (37) recorded ECGs on a sampling frequency equal to 250 Hz. The two systems present a similar configuration with two electrodes composed of conductive yarn and one textile stretchable respiration sensor, completely integrated in a textile belt surrounding the body of either human or horse (**Figure 1**). In addition, a Bluetooth Low Energy (BLE) connection and a long-life battery supply allowed continuous monitoring of the physiological signals. Before starting the S1, both the human and the animal subjects were habituated to the systems for ∼5 min. During this time window, the functionality of the remote control app was also tested.

Data Analysis and Statistics

Heart Rate Variability Analysis

For the ECG and HRV analysis, we employed Kubios HRV analysis software (Biosignal Analysis and Medical Imaging Group at the Department of Physics, University of Kuopio, Kuopio, Finland) and MATLAB R2019 (The MathWorks, Inc.). The first step in the processing of the ECG signals is to determine the R-peaks of the QRS complexes. To this aim, we applied the Kubios built-in QRS detector algorithm based on the Pan–Tompkins method. Accordingly, each ECG was preprocessed through a bandpass filter in the frequency band of 0.05–40 Hz to reduce power line noise, baseline wander, and other noise components, a squaring of the data samples (to highlight R peaks and help the QRS detection) and a moving average filter (with a window width of 150 ms to smooth close-by peaks). The decision rules included amplitude threshold and comparison to expected values between adjacent R-waves. The threshold was adapted every time a new R-peak was detected. Furthermore, possible ectopic or misdetected R-peaks in the derived R-R time series were corrected after visual inspection of each tachogram. Due to the high quality and signal-to-noise ratio of the recorded ECG data, only <0.15% of the R-peaks on average were manually added or removed from the estimated tachogram. Accordingly, the resulting R-R time series did not require any algorithmic preprocessing step, and no outlier signal segments (i.e., excessive artifacts) were excluded for further analyses, but only small manually corrections were applied. The estimated series of R-R intervals were used to calculate the indexes of HRV in both time and frequency domains (38). The extracted HRV metrics aimed at quantifying the cardiovascular dynamics over time to infer with the horse psychophysiological state. Specifically, within each experimental session, we computed the mean value (µRR) and the standard deviation (σRR) of the RR interval series. Given the analogy between σRR and the total power spectrum, it reflects all the cyclic components responsible for variability in the time window. In addition, as recommended by the Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology (39), we computed further standard HRV metrics such as the square root of the mean squared differences between successive RR intervals (RMSSD) and the percentage of consecutive R-R interval differences >50 ms (pNN50). In the frequency domain, we used an autoregressive modeling-based method to estimate the HRV spectra (AR spectrum). The order of the AR model was set up to the default value of 16 (40). Of note, before computing the AR spectrum, the non-evenly sampled R-R interval series were firstly interpolated by means of a cubic spline function. From each AR spectrum, according to the literature (24, 41, 42), we defined two main HRV spectral bands: the low-frequency band (LF, from 0.01 to 0.07 Hz) and the high-frequency band (HF, from 0.07 to 0.6 Hz). The frequency bandwidths were adapted from studies on human heartbeat dynamics to the horse spectral dynamics in order to reflect the sympathovagal nerve activity. Particularly, the HF components of the HRV band are assumed to be solely influenced by the parasympathetic nervous system. In contrast, the LF band is influenced by both the sympathetic and parasympathetic nervous systems. Once LF and HF ranges were defined, we computed the power spectrum in both LF and HF bands (LF power and HF power), the LF and HF frequency peaks (LFpeak and HFpeak), the LF and HF power normalized to the sum of LF + HF power (LFnu and HFnu), the power

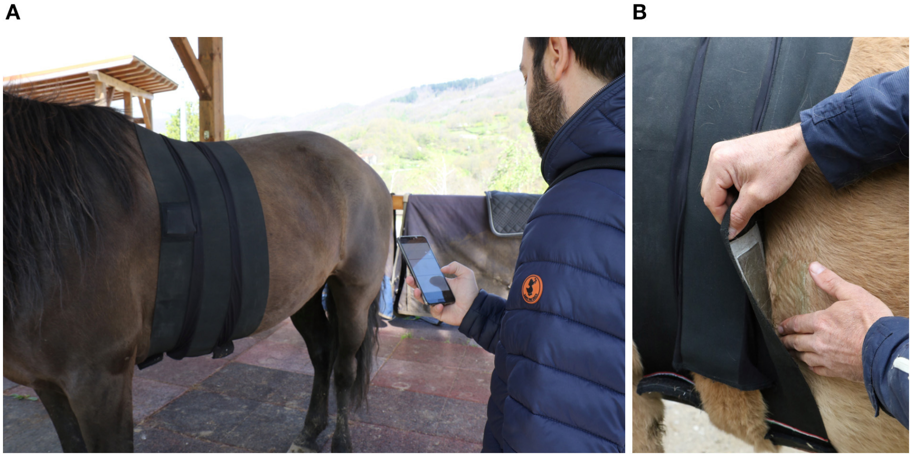

FIGURE 1 | The monitoring system worn by tested horses. In **(A)**, the belt placed on the horse's chest and wirelessly controlled by a mobile app; in **(B)**, one of the electrodes integrated in the elastic belt. Photo by S. Seganfreddo.

in LF band and HF band expressed as a percentage of the total power (LFpower % and HFpower %), and the ratio between LF and HF power (LF/HF). It is worthwhile noting that the LF/HF ratio, which has been frequently used in the scientific literature to assess the sympathetic and parasympathetic balance, has not been fully accepted as an accurate measure of the ANS balance since the LF band also contains parasympathetic dynamics.

Statistical Analyses

According to the experimental paradigm described in the Protocol of Interaction section, each horse performed the same tasks in two different experimental conditions: one while interacting with the familiar human handler and the other one while interacting with an unfamiliar one. Accordingly, each feature was calculated for each experimental session (i.e., S1, S2, S3R, and S3L) in both conditions. Afterward, normalization based on the S1 values, considered baseline, was applied to each feature computed within the S2, S3R, and S3L sessions in order to study the perturbation induced by both the visual and the olfactory interaction (S2n) and also by the human brush (S3Rn and S3Ln) on horse heartbeat dynamics. On the normalized features, two statistical analyses were performed: an intra-set analysis (Φ1) (both for the familiar and the unfamiliar interaction groups) and an inter-group analysis (Φ2). The Shapiro–Wilk test rejected the null hypothesis of Gaussian distribution of the feature samples; therefore, non-parametric statistical tests were adopted.

Φ 1) First, we applied a Friedman test to investigate statistical differences among the three experimental sessions (S2n, S3Rn, and S3Ln) within both familiar and unfamiliar interaction groups. In *post-hoc* analysis, each pair of sessions was compared with each other using a Bonferroni-corrected Wilcoxon signed-rank test to determine significant differences of each pairwise comparison.

Φ 2) Secondly, we investigated statistical differences between the "familiar interaction" and "unfamiliar interaction" for each normalized experimental session S2n, S3Ln, and S3Rn using a Bonferroni-corrected Wilcoxon signed-rank test.

Of note, Friedman test p-values were adjusted through a false discovery rate (FDR) procedure for multiple hypotheses testing (43). Together with the p-value, we reported the effect size of each Wilcoxon signed-rank test ($r = \boldsymbol{Z}/\sqrt{\boldsymbol{N}}$, where Z represents the value of the z-statistics and N is the total number of observations).

RESULTS

In **Table 2**, the median and median absolute deviation (MAD) are reported, calculated among all the horses for each HRV metrics of every experimental task (S2, S3L, S3R normalized by S1) in both experimental conditions (familiar and unfamiliar interactions). Moreover, the *p*-values in **Table 2** represent both the intra- and inter-group statistical results.

The results of Φ1 comparisons (i.e., differences between experimental sessions) showed a significant increase in the horses' mean heart rate (μRR) when both the familiar person and unfamiliar person brushed them (Familiar: $p_{S2n-S3Ln} = 0.014$, $r = -0.448$, $p_{S2n-S3Rn} = 0.002$, $r = -0.475$; Unfamiliar: $p_{S2n-S3Ln} = 0.008$, $r = -0.457$, $p_{S2n-S3Rn} = 0.048$, $r = -0.341$) (**Figure 2**). Contrarily, the horses' heart rate standard deviation (σRR) was subjected to a significant decrease in both familiar and unfamiliar interactions (Familiar: $p_{S2n-S3Ln} = 0.032$, $r = 0.359$, $p_{S2n-S3Rn} = 6.66{\cdot}10^{-4}$, $r = 0.538$; Unfamiliar: $p_{S2n-S3Ln} = 0.003$, $r = 0.475$). Concerning the features in the frequency domain (**Figure 3**), the unfamiliar group showed a significant decrease in LF when the horse was brushed on its left side (S3Ln) in comparison to the exploratory session (S2n) (*post-hoc*-adjusted $p_{S2n-S3Ln} = 0.032$, $r = 0.256$). Also, a significant increase in HF% was recorded in the same experimental condition (S3Ln), still considering the unfamiliar humans' group (*post-hoc*-adjusted $p_{S2n-S3Ln} = 0.021$, $r = -0.354$). Moreover, the HF% revealed a significant increase during the grooming phase on both sides of the horses when the familiar set was considered (*post-hoc*-adjusted $p_{S2n-S3Ln} = 0.048$ $r = -0.413$; $p_{S2n-S3Rn} = 0.008$, $r = -0.336$). Interestingly, HF% and the HF were the only features that showed noteworthy differences in the *Φ*2 statistical analysis comparing the two groups, familiar vs. unfamiliar (HF: $p_{familiar-Unfamiliar} = 0.003$, $r = 0.430$; HF%: $p_{familiar-Unfamiliar} = 0.044$, $r = 0.269$). In particular, both the median variation of the HF power spectra and percentage power spectra significantly increased when a familiar human was grooming the horse on its right side [i.e., during S3Rn (**Table 2, Figure 3**)].

DISCUSSION

Our results show a difference in the horses' heartbeat dynamics during both conditions (familiar vs. unfamiliar person) and through the interacting sessions (presence of a motionless human vs. physical interaction). These findings reflect distinct emotional responses of the animals as implying not only the handler's familiarity with the horse but also the type of interaction he or she may have with it (i.e., contact or contactless). The latter induces a significant decrease in both the mean heart rate (corresponding to an increase in μRR) and its variability (σRR) when horses experience brushing on both sides (**Figure 2**). This could reflect a general decrease in the horse's arousal level related to the brushing task, independent of the familiarity with the human performing the thus-mentioned task. Indeed, to indicate physiological stress, the average heart rate is actually suitable (16), as it is linked to emotional arousal during both situations, positive and negative. However, since this reaction in μRR and σRR does not change as a function of the familiarity level, it is reasonable to think that they can reflect only two different arousal levels (44), which our protocol itself triggered. Previous studies have indeed proven that petting reduces signs of fear in horses and lowers heart rates (45).

Moreover, it is worth noting that the fixed order of the sessions in our protocol allowed the horses to physically investigate the person prior to the grooming session. It is likely this may have helped the horses decrease their state of alert, thus resulting in a more relaxed condition during the final task.

TABLE 2 | Median ± median absolute deviation (MAD) of all normalized features computed in each session and during the interaction with both the familiar and unfamiliar humans.

Feature	**Session**	**Median ± MAD Horse–familiar person**	**Median ± MAD Horse–unfamiliar person**	**Φ2 *P*-values**
μRR	S2n	1.03 ± 3.83e-02	1.04 ± 3.79e-02	p = 0.976
	S3Ln	1.06 ± 4.99e-02	1.08 ± 6.49e-02	p = 0.484
	S3Rn	1.05 ± 5.35e-02	1.05 ± 5.40e-02	p = 0.162
	Φ1 Friedman *p*-value	**p = 1.41e-03**	**p = 7.68e-03**	
σRR	S2n	1.07 ± 0.37	1.32 ± 0.47	p = 0.976
	S3Ln	0.81 ± 0.20	0.75 ± 0.24	p = 0.429
	S3Rn	0.87 ± 0.22	0.79 ± 0.29	p = 0.831
	Φ1 Friedman *p*-value	**p = 8.36e-04**	**p = 4.56e-03**	
RMSSD	S2n	0.97 ± 7.04e-02	0.92 ± 0.14	p = 0.927
	S3Ln	0.94 ± 8.68e-02	0.87 ± 0.17	p = 0.605
	S3Rn	1.03 ± 0.21	0.91 ± 0.17	p = 0.362
	Φ1 Friedman *p*-value	p = 0.840	p = 8.39e-02	
pNN50	S2n	0.95 ± 0.14	0.95 ± 0.11	p = 0.738
	S3Ln	1.03 ± 0.21	0.92 ± 0.11	p = 0.584
	S3Rn	0.99 ± 0.21	0.93 ± 0.19	p = 0.181
	Φ1 Friedman *p*-value	p = 0.663	p = 0.438	
LFpeaκ	S2n	0.80 ± 0.20	1.00 ± 0.33	p = 0.101
	S3Ln	0.86 ± 0.26	1.00 ± 0.33	p = 0.897
	S3Rn	1.00 ± 0.40	1.00 ± 0.50	p = 0.263
	Φ1 Friedman *p*-value	p = 0.762	p = 0.753	
LFpower	S2n	0.84 ± 0.40	1.28 ± 0.66	p = 0.808
	S3Ln	0.87 ± 0.55	0.48 ± 0.36	p = 0.212
	S3Rn	0.93 ± 0.67	0.99 ± 0.68	p = 0.761
	Φ1 Friedman *p*-value	p = 0.309	**p = 0.0327**	
LFpower%	S2n	1.01 ± 0.30	0.95 ± 0.24	p = 0.693
	S3Ln	1.14 ± 0.35	0.92 ± 0.30	p = 0.236
	S3Rn	0.98 ± 0.24	1.05 ± 0.24	p = 0.543
	Φ1 Friedman *p*-value	p = 0.499	p = 0.260	
LFnu	S2n	0.99 ± 0.14	1.03 ± 0.17	p = 0.879
	S3Ln	1.04 ± 0.20	0.93 ± 0.14	p = 0.301
	S3Rn	0.94 ± 0.11	1.05 ± 0.18	p = 0.162
	Φ1 Friedman *p*-value	p = 0.296	p = 0.0646	
HFpeak	S2n	1.00 ± 0.20	1.02 ± 0.19	p = 0.316
	S3Ln	1.00 ± 0.28	1.10 ± 0.25	p = 0.927
	S3Rn	1.07 ± 0.24	1.04 ± 0.41	p = 0.592
	Φ1 Friedman *p*-value	p = 0.703	p = 0.904	
HFpower	S2n	0.84 ± 0.34	0.81 ± 0.20	p = 0.212
	S3Ln	0.82 ± 0.22	0.48 ± 0.26	p = 0.094
	S3Rn	1.11 ± 0.28	0.55 ± 0.30	**p = 3.50e-03**
	Φ1 Friedman *p*-value	p = 0.296	p = 0.0705	
HFpower%	S2n	0.88 ± 0.58	0.64 ± 0.42	p = 0.648
	S3Ln	1.29 ± 0.75	1.13 ± 0.31	p = 0.563
	S3Rn	1.22 ± 0.54	0.77 ± 0.36	**p = 0.044**
	Φ1 Friedman *p*-value	**p = 7.68e-03**	**p = 0.0260**	
HFnu	S2n	1.16 ± 0.48	0.92 ± 0.44	p = 0.693
	S3Ln	0.84 ± 0.40	1.13 ± 0.45	p = 0.879
	S3Rn	1.22 ± 0.46	0.69 ± 0.31	p = 0.059
	Φ1 Friedman *p*-value	p = 0.296	p = 0.0646	

(Continued)

TABLE 2 | Continued

Feature	Session	Median ± MAD Horse–familiar person	Median ± MAD Horse–unfamiliar person	Φ2 *P*-values
LF/HF	S2n	0.79 ± 0.52	1.12 ± 0.71	$p = 0.952$
	S3Ln	1.40 ± 0.87	0.81 ± 0.35	$p = 0.670$
	S3Rn	0.76 ± 0.38	1.60 ± 1.08	$p = 0.181$
	Φ1 Friedman *p*-value	$p = 0.296$	$p = 0.0646$	

P-values in the last column show the results of the Φ2 statistical analysis. Results of the Φ1 comparisons among sessions are shown in the rows denoted as "Φ1 Friedman p-values" for both familiar and unfamiliar groups.

μRR, mean value of the RR interval series; σRR, standard deviation of the RR interval series; HF, high-frequency band; LF, low-frequency band; RMSSD, square root of the mean squared differences between successive RR intervals.

Bold values represent statistically significant p-values.

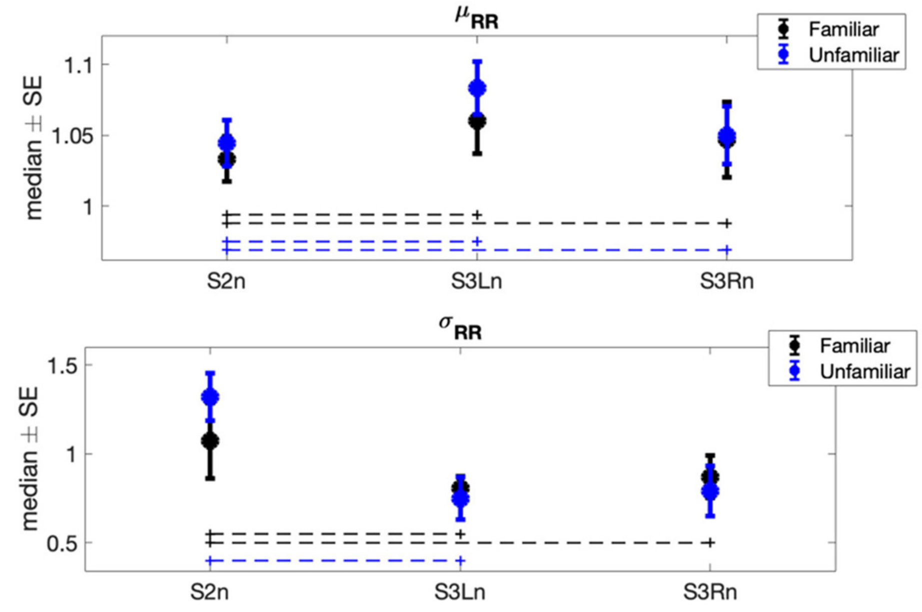

FIGURE 2 | Each error bar represents the median ± standard error (SE) of time-domain normalized features showing at least a significant result in one of the two statistical analyses (i.e., Φ1 or Φ2) in each experimental session. Blue plots are associated with the heart rate variability (HRV) signals recorded during the interaction between horses and the related familiar person; black plots are associated with the HRV signals recorded during the interaction between horses and the related non-familiar person. The dot lines indicate which pair of sessions was significantly different within each group.

The most interesting and relevant results are achieved from the statistical comparison between the familiar and unfamiliar interaction. Specifically, when the familiar humans groomed the horses on their right side, both HF and HF% were significantly higher compared to when unfamiliar handlers were in charge of the grooming procedure. This shift of the sympathovagal balance toward a vagal predominance indicates that the horses experienced relaxation when with humans they knew and while interacting with them. Such results can be the overwhelming evidence of the capacity of horses to recognize familiar humans. In fact, these results constitute the objective measure Proops and McComb proposed (1) regarding the capacity of horses to individually recognize familiar people by cross-modally matching multiple information criteria. Moreover, Proops et al. (46) found that horses, after a single encounter with an individual displaying an emotional facial expression, reacted accordingly to the subsequent interaction with that same person in a neutral context, even after 3–6 h. Lansade et al. (6) showed how horses preferred to touch pictures showing the face of their current or previous keeper instead of a novel unknown face during an experimental trial. Specifically, horses were able to recognize the photograph of a familiar keeper even if they had not seen him or her for 6 months. Besides supporting our results, these studies brought up an additional compelling issue [i.e., the associations between emotions and memory. It has been proven that those events that induce positive or negative emotional state are more easily recalled than those considered emotionally neutral (47)]. Our study reveals that the familiarity with the handler is paramount for the horse to feel comfortable, and this is even truer when the interaction involves a physical contact. Therefore, the contact involving familiar humans likely triggered individual-specific emotional memory in tested horses,

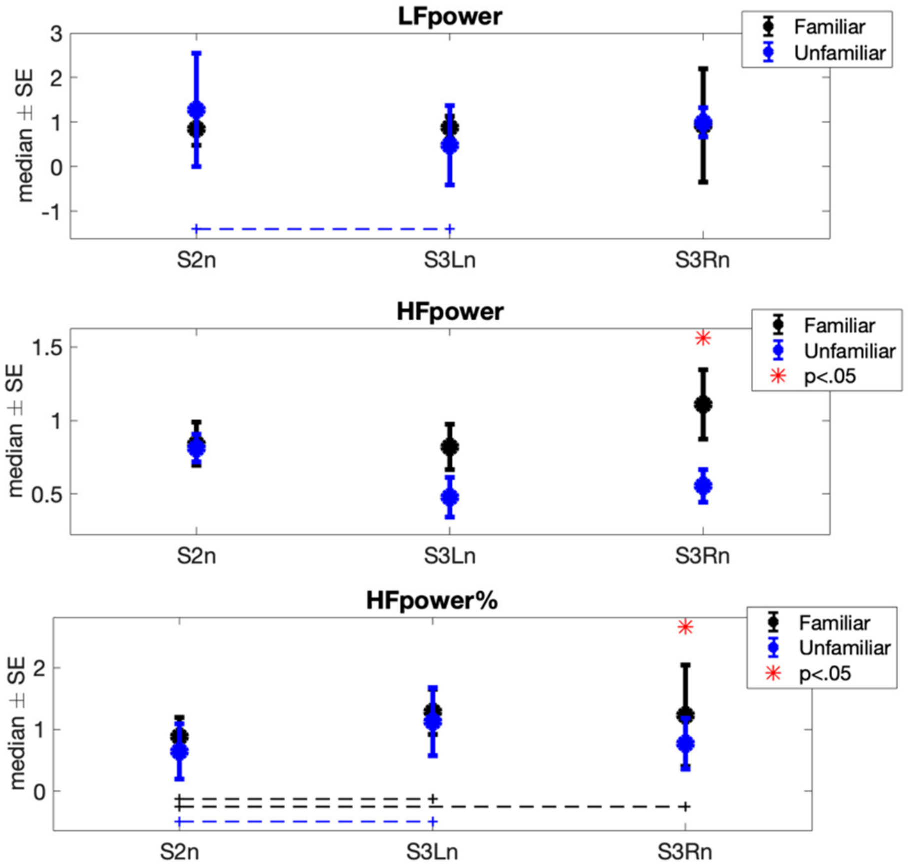

FIGURE 3 | Each error bar represents the median ± standard error (SE) of frequency-domain normalized features showing at least a significant result in one of the two statistical analyses (i.e., Φ1 or Φ2) in each experimental session. Blue plots are associated with the heart rate variability (HRV) signals recorded during the interaction between horses and related familiar person; black plots are associated with the HRV signals recorded during the interaction between horses and the related non-familiar person. The dot lines indicate which pair of sessions was significantly different within each group. The red star shows during which session the statistical comparison between familiar and unfamiliar groups was significant.

which, as suggested by physiological dynamics, presumably has a positive valence.

Interestingly, we obtained significant differences between the two familiarity levels only when the handlers physically interacted with the right side of the horse. Indeed, while familiar interactions induced a significant increase in the HF% when contact occurred on both sides of the horse, the grooming performed by the unfamiliar humans showed a significant increase in the HF% only when performed on the left side. In addition, also concerning the HF index, a strong difference between the two familiarity levels is shown only when right-side contact is considered. It is well-known that handling procedures on domestic horses are traditionally practiced on their left side. Therefore, we hypothesized that the approach on the right side constituted an additional stimulus for tested horses, potentially perceived as an unusual handling position and thus contributing to the increase of their discomfort when performed by an unfamiliar handler.

Following the same logic, the behavior of LF appears conceivable. Although LF does not seem to provide an index of cardiac sympathetic activity (48), it is nonetheless affected by the alteration in the sympathovagal balance after the start of the interaction between human and horse. We could, however, speculate that, due to the increase in HF, the decrease in LF may reflect a shift in the sympathetic tone.

It is important to note that our study relies on a strong standardization of experimental protocols. Two main categories of handling tests have been broadly used so far: the presence of a motionless person who remains still in front of the animal and a slow approach toward the horse itself, leading to physical contact (13). A review of literature regarding horses' reactions to stationary or moving humans (49) reveals that physiological signals are frequently linked to this type of handling test, but usually only considering the horses' average heart rate within a short window as a marker. In a few other cases, cardiac activity has been considered an indicator of emotional states of the horses during interactions with familiar and unfamiliar experimenters; however, handling tests in these studies differed from the ones we implement here [i.e., (50, 51)]. The same handling procedures we used were also employed by Fureix et al. (5), analyzing horses' behaviors with unknown or familiar experimenters, but without collecting physiological variables; in the case of Sankey et al. (52), heart rate alone was monitored. Hence, we here combined an interaction task with three different conditions (no interaction, closeness, and physical contact) with a familiar/unfamiliar human handler test, concomitantly evaluating the effects of these situations on horses' HRV. Even though the finest interpretation of animals' emotional reactions benefits from the incorporation of assorted data, such as behavioral and physiological data, we did not consider horses' temperament or reactivity in the present study. Rather, we focused on how long-term relationships with humans may affect horses' emotional state in daily management activities, which generally involve some sort of contact.

The measurement of either the emotional or affective state of an animal is currently of interest in a variety of fields, such as affective neuroscience, evolutionary zoology, comparative psychology, and animal welfare (53). In particular, the investigation of positive emotions and how to prolong positive affective states in animals both represent promising paths for improving animal welfare (21). Broadening the view on interaction with humans, the possibility to comprehend how an animal is experiencing contact with people is invaluable. Animal-Assisted Interventions (AAIs) may be one field that could benefit the most from this kind of approach. The success of AAI itself is in fact strictly dependent on the affiliative nature and on the emotional involvement characterizing the human–animal dyad (54–56). This work may help in selecting the best procedures in terms of the physical approach of the animal involved in the interventions, in accordance with species-specific behavioral features, and it emphasizes the importance of building a relationship, thus not reducing the interaction to the occasional encounters characterizing the therapy.

CONCLUSION

Our results suggest that a sequence of positive interactions with the same caretaker represents for horses the probable trigger for experiencing presumed positive emotions during the interaction itself. The novelty of this study lies in the possibility to obtain horses' affective assessments, carried out through the objective analysis of their HRV. The opportunity to effectively measure the emotional state of an animal, in multiple conditions including during contacts with other individuals, paves the way for a broad variety of future studies that set the human perspective to the side so as to prioritize that of the animal.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethics Committee of the Experimental Zooprophylactic Institute of Venice (IZSVe). The patients/participants provided their written informed consent to participate in this study. The animal study was reviewed and approved by Ethics Committee of the Experimental Zooprophylactic Institute of Venice (IZSVe) CE IZSVe 07/2020. Written informed consent was obtained from the owners for the participation of their animals in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

PB, AL, CS, and AG designed the experiments and collected the data. AG, AL, and EF analyzed the data. CS, AG, LC, and PB wrote the first draft. All authors finalized the manuscript.

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How Dogs Perceive Humans and How Humans Should Treat Their Pet Dogs: Linking Cognition With Ethics

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Humans interact with animals in numerous ways and on numerous levels. We are indeed living in an "animal"s world,' in the sense that our lives are very much intertwined with the lives of animals. This also means that animals, like those dogs we commonly refer to as our pets, are living in a "human's world" in the sense that it is us, not them, who, to a large degree, define and manage the interactions we have with them. In this sense, the human-animal relationship is nothing we should romanticize: it comes with clear power relations and thus with a set of responsibilities on the side of those who exercise this power. This holds, despite the fact that we like to think about our dogs as human's best friend. Dogs have been part of human societies for longer than any other domestic species. Like no other species they exemplify the role of companion animals. Relationships with pet dogs are both very widespread and very intense, often leading to strong attachments between owners or caregivers and animals and to a treatment of these dogs as family members or even children. But how does this relationship look from the dogs' perspective? How do they perceive the humans they engage with? What responsibilities and duties arise from the kind of mutual understanding, attachment, and the supposedly "special" bonds we form with them? Are there ethical implications, maybe even ethical implications beyond animal welfare? The past decades have seen an upsurge of research from comparative cognition on pet dogs' cognitive and social skills, especially in comparison with and reference to humans. We will therefore set our discussion about the nature and ethical dimensions of the human–dog relationship against the background of the current empirical knowledge on dog (social) cognition. This allows us to analyze the human–dog relationship by applying an interdisciplinary approach that starts from the perspective of the dog to ultimately inform the perspective of humans. It is our aim to thereby identify ethical dimensions of the human–dog relationship that have been overlooked so far.

Keywords: animal cognition, social cognition, animal ethics, human-animal interactions, positive duties, trust

INTRODUCTION

The question of how dogs perceive us humans is important for several reasons, both from the perspective of biologists as well as animal ethicists. First, an enduring topic of animal behavior and animal cognition research is how animals adapt to their social environment, how they cope with the challenges of dynamic relationships among group members, and especially how they achieve a balance between competition and cooperation. Complex social life has been proposed as one of the main driving forces in the evolution of higher cognitive abilities in humans and non-human animals (Humphrey, 1976; Dunbar, 1998).

Secondly, while evolution has equipped species with the appropriate cognitive tools to engage in sophisticated social interactions during foraging and conflict management, including the formation of valuable relationships (social bonds), it is less clear how species became able to deal with heterospecifics with whom they live in close interaction, i.e., not simply as prey or predator. This is the case in at least two domains, in urban species and in domesticated species. In the latter domain, dogs have been considered as the species that formed the closest bonds with humans. So how was it possible for these animals to engage in such close interactions with humans, who are members of a different species, with a different anatomy, physiology, including different sensory modalities, behavior, and cognition?

While the first two reasons might inspire cognitive biologists who address topics in animal behavior and evolution to investigate dogs' perspective on the human–dog-relationship, animal ethicists might find additional reasons why the question of how dogs perceive humans is important. This is because the relationship between humans and dogs is characterized by a clear dominance hierarchy, not only during the process of domestication, but also during the individual life of the dog. This only gives us an ethical reason why to consider the human–dog-relationship but also a reason why to consider it differently than relationships that are not characterized in such a way. Humans have domesticated dogs, not vice versa, mainly to exploit them for their own benefit, as assistants during hunting, as guardians of their homes, or as companions. More recently, we have added other tasks and purposes that cover a very wide range of different contexts. We use dogs as testing devices in labs, as search (and rescue) animals (when looking for missing persons as much as when looking for rare truffles), as therapists in animal-assisted therapies, dance partners in dog dancing, hair models in dog grooming, or influencers in social media, just to name a few. The multitude of interactions and contexts in which we use them, of course, has produced a number of welfare issues and, as we are going to argue, ethical issues beyond welfare. While ethical debates have convincingly pointed to human responsibilities for example in the case of farm animals and lab animals, companion animals are often not so clearly seen as animals which we "use," objectify, or instrumentalize, maybe because the term "companion" indicates to some degree a mutual relationship rather than an exploitative one. But how, in fact, do dogs experience this relationship? How do they perceive the humans they engage with? Have they indeed specifically adapted to interact and form "special" bonds with humans as the Domestication Hypothesis (see our section on Effects of Domestication) suggests? We assume that part of the answer to these questions can be found in the growing evidence for dogs' special skills to perceive and understand us.

The structure of this paper is as follows. In a first step, we will discuss insights from the dog's domestication history and from empirical studies on their (social) cognition to illustrate how dogs perceive us, and consequently sketch the nature of our relationship with them. In a second step, we will assess what ethical responsibilities arise from the characteristics of the human–dog relationship. Should we profoundly reevaluate some ways we use dogs, and enrich the narrative of dogs as "companions" and "man's best friend" with some ethical considerations that are indeed more demanding? Our methodology thus utilizes the results from current debates in dog social cognition to evaluate the human–dog relationship from a critical, ethical perspective. Our aim is to show by means of such an interdisciplinary investigation in what ways our current knowledge about dog domestication and dog social cognition can and should inform our treatment of these animals. For our discussion of the empirical evidence, we have picked three areas of dog social cognition where we find a substantial amount of studies. Our selection thus mirrors the general interest of the research community. However, the community might be neglecting other possible abilities in dogs due to a lack of interest in them, a publication bias towards positive results, flawed study designs or other reasons. We will come back to this in our ethical discussion, since what we do not know about dogs might be relevant to the treatment that we owe them. While in this paper we will restrict our discussion of ethical implications to the kinds of studies available, other, more profound ethical implications might lie ahead, once cognition research broadens its focus.

CHARACTERIZING THE HUMAN–DOG RELATIONSHIP: BIOLOGICAL PERSPECTIVES

In this section, we will investigate the characteristics of the human–dog relationship by following the decisive question of how dogs adapt to the human environment. We will turn our attention to the latest research results from the fields of animal cognition and behavior. The default assumption is that dogs' skills are firmly based on some general canine abilities of intraspecies communication plus a combination of phylogenetic and ontogenetic abilities of interspecies communication. The latter ones have emerged from domestication and individual social and cognitive development (Huber, 2016). Both kinds of developmental factors have contributed to the success of dogs living among and with humans, including their adoption of the numerous roles humans give to them.

Effects of Domestication: New Skills or Special Sensitivity?

For thousands of years humans have changed the morphology, physiology, and behavior of dogs through selective breeding.

Canines were the earliest domesticated animal, a process that started somewhere between 15,000 and 30,000 years ago, most likely when gray wolves began scavenging around human settlements. Dog experts differ on how active role humans played in the next step, but eventually the relationship became a mutual one, as we began employing dogs for hunting, guarding, and companionship.[1]

It is, however, still an open question to what extent the three kinds of cognitive and communicative adaptations – of the wolf, the dog, and the human companion (pet) – contribute to this extraordinary achievement. It is furthermore disputable if the outcome of these different developments is a new skill or rather a special sensitivity. In addition, we may distinguish not only between phylogenetic and ontogenetic routes, but also between construction and inflection (Heyes, 2003), to overcome the simplistic dichotomy of nature vs. nurture. One cautionary application of the multiple routes framework would be to assume that dogs have acquired a special sensitivity towards human gestures, speech, and behavior as a phylogenetic inflection through human selection over many thousands of years. This sensitivity is not a new cognitive or sensory mechanism, but the result of a selection biasing the input.

Since the time dogs became a special focus of ethology and comparative cognition research, the so-called Domestication Hypothesis has dominated the debate about the special skills of dogs (Hare et al., 2002; Topál et al., 2009; Miklósi and Topál, 2013). It has been assumed that dogs have been selected to cooperate and communicate with humans during domestication and, thus, evolved some genetic predispositions allowing them to develop skills shared with humans. Accordingly, it has been suggested that, in a unique way, domestication has equipped dogs with two abilities necessary for cooperative problem solving – namely social tolerance and social attentiveness, which enable them to adjust their behavior to that of their human partners (Ostojic and Clayton, 2014).

Empirical support for the Domestication Hypothesis has been sought by comparing dogs and wolves. Several of the early comparisons have indeed found profound differences between domesticated forms and their wild ancestors (i.e., the closest wild-living relatives) in the way they communicate and cooperate with humans, for instance in following human gestures, as well as in their capacities for social tolerance and social attentiveness. It has been proposed that dogs have been selected for tamer temperament and for reduced fear and aggression, which allows a potential partner to come close even around food, which in turn explains the higher success of dogs in cooperative and communicative interactions with humans in comparison to wolves (Hare and Tomasello, 2005).

Apart from social tolerance, cooperation with humans and learning from humans are facilitated by a high degree of social attentiveness. Cooperation requires that the partners pay sufficient attention to each other in order to adjust or synchronize their behavior, and social learning requires paying attention to the demonstrator's actions and the context in which they are executed (Huber et al., 2009). Attentiveness towards potential partners varies not only according to the tasks, but at least in the human–dog case, it crucially depends on the relationship between the partners (Range et al., 2007; Horn et al., 2013). Dogs have proven successful in several tasks that are thought to require high attention towards humans, such as experiments on social learning (Kubinyi et al., 2003; Topál et al., 2006; Huber et al., 2009, 2014; Range et al., 2011; Fugazza and Miklósi, 2014), social referencing (Merola et al., 2012a,b), communication (Virányi et al., 2004; Schwab and Huber, 2006; Udell and Wynne, 2008; Dorey et al., 2009; Kaminski et al., 2012), responding to unequal rewards (Range et al., 2009), and cooperation (Naderi et al., 2001; Bräuer et al., 2013; Ostojic and Clayton, 2014).

Another line of evidence for the differences between dogs and wolves comes from pointing studies. Young dogs follow human pointing better and look at humans more readily than human-raised wolves (Miklósi et al., 2003; Gácsi et al., 2009). This led researchers to propose that dogs have developed increased social attentiveness compared to wolves and, thus, can achieve more complex forms of dog–human communication and cooperation than wolves (Miklósi et al., 2003; Virányi et al., 2008).

However, as most of the studies compared the animals' interactions only with humans (Hare et al., 2002; Miklósi et al., 2003; Topál et al., 2005; Udell and Wynne, 2008; Virányi et al., 2008; Gácsi et al., 2009; Udell et al., 2011), it remained unclear whether the differences between dogs and wolves reflect mere differences in the readiness of dogs and wolves to interact with humans or more fundamental differences regarding intraspecific cooperation. Indeed, experiments at the Wolf Science Center in Austria have shown that (hand-raised) wolves pay as much attention to human partners as dogs do and that these wolves can even outperform dogs in learning from observation of a conspecific, indicating the high social attentiveness of the species (Range and Virányi, 2013, 2014). Accordingly, the so-called Canine Cooperation Hypothesis postulates that dog-human cooperation evolved on the basis of wolf–wolf cooperation and that no additional selection for social attentiveness and tolerance was necessary to allow for dog-human cooperation to evolve (Range and Virányi, 2014, 2015; Virányi and Range, 2014). Rather than tolerance, domestication may have led to reduced fear of humans, which is supported by the fact that dogs need less intensive socialization than wolves to avoid fear of humans (Scott and Fuller, 1965; Klinghammer and Goodmann, 1987). If dogs are less fearful of humans and more comfortable around them than wolves, they would have gained advantages from witnessing human actions (even without being more attentive), and from sooner engaging in interactions with humans.

According to the Canine Cooperation Hypothesis, the high social attentiveness, tolerance, and presumable cooperativeness of wolves provided a good basis for dog–human cooperation to evolve during domestication. In addition, some relevant features in sociability and cooperativeness are shared by wolves and humans and thus have probably facilitated the domestication

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[1] There is the possibility that dogs "domesticated themselves" to exploit a niche associated with the anthropogenic environment. However, given humans' interest in domesticating (and then breeding and keeping) all sorts of species for their purposes we find it hard to believe that in dogs it was a one-sided process with all agency ranging on the dog's side.

of dogs (Clutton-Brock, 1984; Schleidt, 1998). However, dogs are not only specifically sensitive to humans because of the domestication history of their species and the evolutionary baggage that has been passed down to them from their wild ancestors, the wolves. They are also what they are because each of them trains their outstanding sensitivity towards humans on an individual, ontogenetic level.

Individual Development

Despite being equipped by evolution with skills and propensities to adapt to humans by showing high levels of social tolerance and attentiveness, dogs need to individually learn much about their heterospecific partners in order to establish and maintain firm individualized relationships. During their life in the human household as pets or companions, they have ample opportunities to do so. Family dogs live in close day-to-day contact with humans and can therefore collect an enormous amount of experience. Research from the last decades has sought to understand how dogs perceive elements of their environment, learn about it, and use this knowledge to make informed decisions about proper behavior (Huber, 2016). Their skills in face processing, behavior reading, observational learning, and perspective taking play a crucial role here (for reviews, see Bensky et al., 2013; Kaminski and Marshall-Pescini, 2014; Lea and Osthaus, 2018). In what follows, we will summarize recent findings on dogs' understanding of human emotions, gestures, and actions.

Understanding Human Emotions: How Dogs Read Our Faces and Listen to Our Voices

Interspecies emotional communication is in part facilitated by chemosignals (D'Aniello et al., 2018), but, faces are in addition an important visual category for many species because they provide a rich source of perceptual cues, including many idiosyncratic features, and thus facilitate important discriminations. In the specific case of dogs, it has been suggested that their increased readiness to look at the human face provides a basis for complex forms of dog-human communication (Miklósi et al., 2003). By monitoring human faces, dogs seem to obtain important social information, ranging from communicative gestures to attentive states (Schwab and Huber, 2006; Kaminski and Nitzschner, 2013). Dogs can quickly find out what features are relevant or informative for making important decisions. They also spontaneously focus on the eyes to infer where humans attend, what they are interested in, and even what they intend to do next (see eye movement studies like for example Somppi et al., 2014).

Gaze following is present in many species, but dogs outperform even nonhuman primates in following human gaze in object choice tasks (Hare et al., 2002; Cooper et al., 2003). Like in the case of human infants, their gaze following is modulated by ostensive cueing, such as direct gaze and addressing by the person, which is evidence that it is more than simply a product of reflexive and learnt mechanisms (Téglás et al., 2012). Dogs also follow human's gaze into distant space (Wallis et al., 2015), and they use the eyes of humans to judge their attentional state. In one study, dogs were tempted with sausages but told by the caregiver not to take them. The dogs obeyed more or less depending on the caregiver's attention to them (Schwab and Huber, 2006). When being watched by the caregiver, dogs stayed lying down most often or for the longest time, but when the caregiver read a book, watched TV, turned her back on them, or left the room, their patience ceased. Obviously, they were using eye contact and eye orientation as cues.

Human faces provide much more information than simply looking patterns. A great number of idiosyncratic features allow humans to identify and recognize others. Would dogs also profit from this rich source of information? Could they also identify and recognize their caregiver and other familiar humans? In one study we put these questions to test and asked dogs to discriminate between their caregiver and another highly familiar person by active choice (approaching and touching; Huber et al., 2013). The task could not simply be solved on the basis of familiarity (approaching the familiar person), which is considered an easier task (Wilkinson et al., 2010), but required a fine-grained distinction of familiar people. Dogs could do so, even when they saw only the (real) face of the humans, but had difficulties when the face was only projected as a picture to a big screen. Only a minority of dogs could finally identify the caregiver on face pictures in which the outer parts of their faces were occluded with a balaclava hood. A further study confirmed the importance of human eyes for dogs, because they rely less on the nose or the mouth than on the eyes for human face discrimination (Pitteri et al., 2014). They also prefer looking at upright over inverted faces, exactly as we ourselves do (Somppi et al., 2012, 2014).

On the basis of our findings that dogs are competent enough to extract subtle, idiosyncratic features of a face in order to identify a human person, despite changes of color, hair style, make-up, jewelry, hats, etc., we went one step further and asked whether dogs may also learn from our facial expressions. It has been already shown that dogs can rely on human facial expressions when making decisions about approaching other objects (Merola et al., 2012a). However, a study in which the stimuli were photographs showing human faces with two different emotional expressions did not yield conclusive results (Nagasawa et al., 2011). Although dogs learned to discriminate between happy (smiling) faces and neutral faces of their caregiver and subsequently transferred the contingency to novel faces of unfamiliar people, it is not clear whether the dogs simply used a salient discriminatory cue, such as the visibility of teeth in the happy faces, to solve both the discrimination and the generalization task.

In the Clever Dog Lab in Vienna, we asked dogs to discriminate "hemifaces" – either the lower or the upper half of the faces – of women showing different (happy and angry) emotions. With this trick we could investigate whether dogs solve the task solely by attending to the emotional expression rather than any inadvertent cues in the presented human face (Müller et al., 2015). Given that the simple discriminatory cues in one half of the faces – such as teeth in the lower half – were absent in the other half, the authors could test the dogs' ability to spontaneously categorize novel pictures on the sole basis of the emotional expression, provided globally and not just by local cues. Indeed, the dogs did not only manage to learn the training task, but they were also able to transfer the extracted rule to novel faces, even if they had been presented a hemiface not shown in training.

These findings provide strong evidence that dogs are able to discriminate between emotional expressions in a different species, which, compared to emotion recognition in conspecifics, is particularly challenging (cf. Parr et al., 2008). For instance, humans open their mouth and show their teeth while laughing, whereas dogs express the underlying emotions of aggression by showing their teeth. Therefore, dogs cannot rely on genetic predispositions, but need to individually learn the emotional expressions of humans. The fact that dogs could spontaneously generalize from one face half to the other without the possibility to use cues learned during training strongly supports the idea that they remembered something from their daily experiences with their caregiver or other familiar people and then used this information in the artificial laboratory environment. As they had not been explicitly trained, it seems that they had acquired the competence by latent learning.

Humans express their emotions not only visually but also their voices convey information about affects. Dogs may exploit these contingencies by extracting and integrating bimodal sensory emotional information from humans. From the combination of visual and auditory cues they may form multimodal representations. Using a cross-modal preferential looking paradigm, researchers at the University of Lincoln (United Kingdom) managed to show that dogs spontaneously combine human or dog faces with different emotional valences (happy/playful versus angry/aggressive) with a single vocalization from the same individual of the same positive or negative valence (Albuquerque et al., 2016). This result points to the possibility that dogs recognized or understood the emotional content of the human faces, not just discriminated them perceptually. Recent eye-tracking studies have supported this hypothesis (Barber et al., 2016; Somppi et al., 2016).

The ability of dogs to integrate information of humans across modalities has also been investigated by using the expectancy-violation procedure (Adachi et al., 2007). A photograph of either the caregiver's face or an unfamiliar person's face was presented to the dog after a vocalization was played. The vocalization used was from the same person or another person, thus matched or mismatched the image. According to the expectancy-violation logic, dogs should be surprised if the visual and auditory cues mismatch and thus look longer than when the two cues match. This is what happened. After hearing the caregiver's voice when the face of an unfamiliar person appeared (incongruent condition), dogs exhibited extended looking, while in the case when the vocalization and face matched (i.e., came from the same person; congruent condition), the duration of their gaze was comparably briefer. These findings lend support to the hypothesis that dogs recall their caregiver's face upon hearing the caregiver's voice.

Taken together, there is cumulating evidence that dogs obtain social information from their experiences with humans, specifically from their facial expressions. They can recognize and remember individual humans. They understand to a significant degree what these humans attend to, what they are interested in, and what they intend to do next. They can discriminate, individually learn from, and categorize emotional expressions, and they integrate information coming from vocalizations into their understanding of humans and their emotions. Thus, they form multi-modal representations of humans and their emotions, integrating emotions, facial expressions, and vocalizations.

Understanding Human Gestures: How Dogs Learn to Cooperate

Due to domestication programs that had the goal of producing companions that work with or for humans, and thereby follow human commands, dogs may have acquired a special sensitivity to human gestures, speech, and behavior (Miklósi and Topál, 2013). Neither the chimpanzee, humans' closest living relative, nor the wolf, dogs' closest living relative, can understand and use human communicative cues as flexibly as the domestic dog (Kaminski and Nitzschner, 2013). This kind of phylogenetic enculturation that took place over thousands of years is continued and amplified in the course of their lifespan, as companion dogs collect an enormous amount of experience during their life with humans (Topál et al., 1998; Udell and Wynne, 2008, 2010; Topál and Gácsi, 2012). A prominent example of how well dogs understand humans and how eager they are to cooperate is the behavior of assistance dogs, especially for leading blind people (Naderi et al., 2001). In the latter case, information is not only provided but also accepted by both parties in the course of their joint actions. So what exactly do dogs learn about our behavior, especially about human actions that are unlikely in their species-specific action repertoire? An especially interesting group of actions are those that serve us humans to inform the dog or to guide them.

One of the best examples of dogs' socio-cognitive skills is their ability to properly respond to human cues in a cooperative search context. Numerous studies have shown that dogs can reliably follow a set of basic human cues (e.g., distal/proximate pointing, head turns, and eye glances), as well as being adept at flexibly generalizing this behavior to relatively novel human movements (e.g., "cross-pointing," leg pointing, gestures with reversed direction of movement, and different arm extensions; Soproni et al., 2002; Udell et al., 2008). In contrast, substituting the hand with a stick or preventing the dog from seeing the hand protruding from the body contour decreased performance, thereby pointing to the importance of the human's hand. In addition to questions about the cognition involved in dogs' responding to human cueing, experiments have flourished that systematically tested the contexts, the time-course, breed differences, training effects, and other aspects of this canine competence (review in Bensky et al., 2013).

Among those actions, perhaps the best studied one is the human pointing gesture. First of all, pointing by humans is a social cue, which in general is more salient or effective than non- social cues like visual markers in terms of signaling the location of something important, like food (Agnetta et al., 2000; Udell et al., 2008). In sharp contrast to apes (Herrmann and Tomasello, 2006), this ability to use human cues by dogs is more effective in cooperative contexts (Wobber and Hare, 2009) than in competitive ones (Pettersson et al., 2011).

Although so far there is no consensus among researchers about when exactly dogs become competent at understanding the pointing gesture (e.g., Dorey et al., 2010), it is obvious that individual learning is very effective. Even hand-raised adult wolves are as successful in relying on distal momentary pointing as adult pet dogs (Gácsi et al., 2009). Still, positive feedback processes (both evolutionary and epigenetic) have increased the readiness of dogs to attend to humans, providing the basis for dog-human communication. Among dogs, breeds that have been historically bred for working purposes respond to human pointing cues significantly more than breeds that have been bred for companionship (Wobber and Kaminski, 2011), and breeds that were originally bred for cooperative work (e.g., herding) performed better than those that were bred for independent work (e.g., guarding; Gácsi et al., 2009). Furthermore, those with a special training for responding to cues from a distance, like working-gun dogs, utilized a pointing cue significantly more than dogs without such training (McKinley and Sambrook, 2000). Independent of breed differences, shelter dogs are less successful than pet dogs at following a distal momentary-pointing gesture (Udell et al., 2008).[2] Lastly, dogs' future use of human cues is highly malleable depending on reinforcement history (Elgier et al., 2009). All of this does not mean that breed differences (to the extent they exist) are either phylogenetic or ontogenetic – they are most likely both. We should keep this in mind in order to avoid the nature–nurture fallacy.

After the first wave of research on dogs' understanding of human cues, the last decade has devoted work to the question of how subtle (and perhaps unintentional) human cues impact communication interactions between dogs and human (e.g., Kupan et al., 2011; Kis et al., 2012; Marshall-Pescini et al., 2012). Furthermore, researchers have attempted to find the key components or features of the human pointing gesture that contribute to dogs' understanding of it as a communicative action. It may come as a surprise that it is still not clear whether dogs understand the communicative intent of the signaling human or whether they react only to some cuing that directs their attention to the reward. Earlier work showed that dogs are able to rely on relatively novel gestural forms of the human communicative pointing gesture and that they are able to comprehend to some extent the referential nature of human pointing (Soproni et al., 2002). However, recent advances in this research indicate that dogs do not necessarily interpret pointing informatively, that is, as simply providing information, but rather as a command, ordering them to move to a particular location. In one study, dogs ignored the human's gesture if they had better information, and followed children's pointing just as frequently as they followed adults' pointing (and ignored the dishonest pointing of both), suggesting, according to the authors, that the amount of own knowledge but not the level of authority affected their behavior (Scheider et al., 2013). Both findings suggest that dogs do not see pointing as an imperative command but as an informative or referential cue. This does not mean, however, that dogs use higher levels of reasoning to understand the signal, the more parsimonious explanation is that dogs follow human pointing based on associative learning mechanisms, having learned in their individual ontogeny that the human's pointing is often connected to rewards (e.g., Wynne et al., 2008; Dorey et al., 2010). Still, ongoing research is looking into the question of whether dogs react to human pointing gestures in acts of joint communication and shared information.

The latter account of dog's understanding of human behavior is interesting with respect to the meanwhile hotly debated question of whether dogs, like humans (Tomasello et al., 2005), understand other individuals' communicative intent based on some understanding of them as mental agents. Less than a decade ago, the majority of dog researchers were rather skeptical in this respect, assuming that dogs' interpretation of referential behaviors is based on a fairly restricted set of cues (for instance, Wobber and Kaminski, 2011; Kaminski et al., 2012). They were inclined to propose non-mentalistic accounts, which they thought would be sufficient to explain dogs' skills with human communication and enough for guiding dogs' movements within space. Indeed, nothing more would be needed to use dogs during certain activities like hunting and herding.

Still, the area between a completely mechanistic and a completely mentalistic account is huge. At the middle ground we may see dogs being sensitive to humans having visual perspectives that are different from their own. For instance, Bräuer et al. (2004) confronted dogs with a situation in which they were forbidden to take a piece of food. Dogs stole significantly more food if they could be seen by the human, even only through a hole in the wall, showing that to some extent dogs seemed to be sensitive to the human's visual perspective (Bräuer et al., 2004; Kaminski et al., 2009). But is this sensitivity simply a result of associatively learning to respond to direct cues (e.g., the human can be seen), or can dogs infer from indirect cues what humans can or cannot see? The results of two recent studies indicate the second possibility. In a food-stealing task dogs seem to understand that, when the food (and therefore the area around it) is illuminated, the human can see them and, therefore, they refrain from approaching and stealing the food (Kaminski et al., 2013). In the second study, dogs showed that they can understand something about a human's perspective, because, out of two humans informing of where food was hidden, they relied on the one who could see the food hiding process (Maginnity and Grace, 2014). In this famous "Guesser–Knower task" (Povinelli et al., 1990), dogs used cues directly related to the humans' visual access to the food, like whether their eyes were open, whether they were directed to the hiding locations, and whether the informant remained in the room during the hiding.

Very recently we replicated the second study, but added a condition in which no directly observable cues could tell the dogs who would be the knower and thus reliable informant (Catala et al., 2017). The critical control for behavior-reading, as the less demanding alternative to mind-reading, involved two informants that showed identical looking behavior during the food hiding event. However, due to their different position in

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[2] We do not want to go into possible reasons for this, however, it needs to be noted that a whole range of different reasons for this could exist. After all, a household is a very different environment than a shelter. It is possible that it shapes the dog's cognitive abilities. Likewise, their abilities (or perceived lack of abilities) might already have been a reason why their caregivers abandoned them.

the room, only one had the opportunity to see where the food was hidden by a third person. Using geometrical gaze following, dogs could infer who could possibly see the food hiding, and whom to trust. By choosing the help of the knower but ignoring the help of the guesser dogs showed perspective taking.

We still have to be careful and avoid over-interpretation. Geometrical gaze following, despite being seen to rest on a cognitively sophisticated mechanism (Fitch et al., 2010), does not require mind-reading; the recognition of mental states like beliefs, desires, and intentions. The dogs' confidence in the informant who was in the position to see the relevant event (food hiding) might be a product of generalization from similar situations in everyday life (Udell et al., 2011). Still, even this does mean something: dogs seem to observe humans closely, form behavioral rules from this and apply them to new contexts. The reluctance of dogs to follow the looking-away person could have been learned in similar, but not identical, situations during their life in the human vicinity. In numerous cases they have seen what consequences human looking behavior has, that it is easier to communicate with humans whose eyes are visible and who look at instead of away from a target, and that they ignore things they have not seen before. It becomes obvious that living with humans puts a lot of intellectual baggage on the individual dog's learning history. This means, on the other hand, that in order to deal with humans, dogs need opportunities to be with them, observe them, and learn from situations. Still, more research about what dogs understand about the intentions and even beliefs of humans is necessary to confirm dogs' recent inclusion in the small circle of models of non-human perspective taking in a cooperative and hetero-specific context.

Taken together, these findings show us that dogs are sensitive to human gestures, can learn their meaning, and seem eager to cooperate. They understand gestures as imperative commands but also to some extent as informative or referential cues, engaging with humans as communicative partners. Thereby, they do not necessarily subordinate their own perspective to the human one: they take their own (well-informed) knowledge into account when given (ill-informed) commands. Especially dog breeds that have been bred for cooperative work are very good at understanding human gestures and commands. On the other hand, individual training opportunities seem important: shelter dogs for example are less successful than pet dogs at following human pointing gestures. Furthermore, the dogs' reinforcement history shapes their understanding of human gestures. Dogs have been found to be excellent behavior-readers if given the opportunity. They are highly competent in learning about directly observable but also quite subtle behavioral, gestural, vocal, and attentional cues, which is of high adaptive value for life in the human environment. In addition to their behavior-reading competences they also seem to be sensitive to some mental states in humans. They for example seem to know that humans have visual perspectives different from their own.

Understanding Human Actions: How Dogs Learn Our Social Game

Dogs have impressive capacities for social learning. This competence shines through in almost all forms of social learning, including local enhancement (e.g., Mersmann et al., 2011), stimulus enhancement (e.g., Kubinyi et al., 2003), emulation (e.g., Miller et al., 2009), motor imitation (e.g., Huber et al., 2009), selective imitation (Range and Huber, 2007), and deferred imitation (e.g., Fugazza and Miklósi, 2014). They not only benefit from having the opportunity to learn from humans, they actually learn something relevant. For instance, they learn to make a detour to find food (Pongrácz et al., 2001), learn how to manipulate objects (Kubinyi et al., 2003; Pongrácz et al., 2012), and learn the direction in which a sliding door has been pushed to get some treats (Miller et al., 2009). In addition, they are able to anticipate the caregiver's action, and as a result they synchronize their behavior with that of their caregivers (Kubinyi et al., 2003; Duranton et al., 2017). This implies that their learning is not only shaped by goal-directedness but influenced by other factors as well. This even applies to strategies that are seemingly unproductive or dysfunctional but nevertheless used by someone they observe.

Only recently it has been shown that dogs engage in what has been termed "overimitation," the copying of unnecessary or causally irrelevant actions (Lyons et al., 2007). This peculiar form of copying was until that time considered a uniquely human capacity, which likely played a key role in why human culture can accumulate over time (Clay and Tennie, 2018). It had been assumed that humans overimitate not only for cognitive and normative reasons, but also to satisfy social motivations. They attempt to "affiliate with or be like the model" (Nielsen, 2006; Keupp et al., 2013, 393). If dogs show this behavior as well, it could highlight how deep they are enculturated in our human world because their readiness to overimitate could highlight their affiliation with closely bonded humans as a motivation for behavior.

A first study with canines provided suggestive evidence for overimitation (Johnston et al., 2017). In the test, the experimenter first established a positive relationship with the subjects by feeding them and then demonstrated how to open a puzzle box, but also performed a causally irrelevant action onto the box (moving a non-functional lever). Surprisingly, half of all tested dogs and dingoes copied both actions, although in further tests some stopped replicating the irrelevant action.

In two studies in the Clever Dog Lab in Vienna, the two actions had been separated both spatially and temporarily in order to ensure that the dogs did not confuse their causal natures (Huber et al., 2018, 2020). The causal action consisted of opening a sliding door that blocked the access to a treat; the irrelevant action involved touching colored dots that were mounted on the wall at a distance. Touching the paper sheet had no effect and was not necessary for getting the treat. Despite its irrelevance, almost half of the dogs replicated the touching action (Huber et al., 2018).

Before dogs had been tested on overimitation, several studies with great apes failed to show similar effects; they did not even show a tendency to copy the demonstrator's actions that were not necessary to achieve a goal (e.g., Clay and Tennie, 2018). Chimpanzees, for instance, were found to act in a purely goal-directed, efficient manner (Horner and Whiten, 2005). This led Huber et al. (2018) to assume a social rather than a cognitive explanation for overimitation in dogs. Not only their ability to cooperate with, but also to learn from, humans seems to be closely related to their affiliative (e.g., Topál et al., 1998) and communicative (e.g., Miklósi et al., 1998) behaviors towards humans. Dogs seem to interpret a test situation as a form of communication or social game (Soproni et al., 2001), especially when the human experimenter uses ostensive cues (Kubinyi et al., 2003; Topál et al., 2009; Téglás et al., 2012; Wallis et al., 2015). And, like children, they attend more to those humans with whom they also had a close relationship (Horn et al., 2013).

In a follow-up study, we tested the hypothesis that dogs are more inclined to copy irrelevant actions if shown by the affiliated caregiver rather than by an unfamiliar person. By faithfully replicating Huber et al. (2018), using the identical methods and procedures, but only substituting an unfamiliar person for the dog owner as the demonstrator, we found a measurable decrease in the number of dogs that copied the irrelevant action (Huber et al., 2020). This finding thus confirmed our hypothesis that overimitation is facilitated by the affiliative relationship between the human demonstrator and the imitating dog, satisfying social motivations. Family dogs may repeat the actions of the human partner either because they want to please their caregiver or because they are inclined to obey by following tacit commands. While the first is clearly a positive characteristic of the dog–human relationship, the second one is ambiguous, although the two are linked. However, it is also possible – although difficult to prove – that the dogs overimitate because they want to be part of our social game, meaning that they want to be included in the social interaction that is happening. This interpretation is based on the assumption that they could have a social motivation to affiliate with the model and want to "be like the model" – as has been proposed in the case of humans to explain their readiness to overimitate (Nielsen, 2006; Keupp et al., 2013, 393). Here, to "be like the other" could mean that the dogs want to *behave* like the other and *be with* the other. This explanation is compatible with the existence of an urge to please the caregiver or an inclination to obey. The intention to preserve and foster the bond between human and dog, however, may be in itself a motivation behind this behavior. A dog might furthermore trust her caregiver in such a profound way that she sticks to whatever the caregiver proposes, at least for a while. Thus, it takes her some time to detach from the caregiver's irrelevant strategy and come up with a more efficient one herself. In a team that is usually built on trust and affiliation this makes sense as a social strategy. It is surely difficult to test for such explanations based on trust or affiliation, but that should not be a reason to rule them out right from the beginning. Complex social motivations in animals are clearly getting increased attention from empirical research lately. Disentangling the affiliative bonds between dogs and their caregivers, their scope and meaning, is one of the big challenges we face.

Cumulating evidence suggests that the relationship between companion dogs and their human caregivers bears a remarkable resemblance to the parent-infant attachment bond (Archer, 1997; Topál et al., 1998; Gácsi et al., 2001; Prato-Previde et al., 2003; Hare and Tomasello, 2005; Prato-Previde and Valsecchi, 2014). This affiliative bond changes dogs' behavior in multiple ways. It enables dogs to engage their caregiver's caregiving system, and it affects the way the dog explores objects and performs in cognitive tasks (Horn et al., 2012, 2013). Like in children, the bond not only changes the dog's general attitudes towards humans, it is also selective. For instance, dogs pay more attention to the actions of their caregivers than to the actions of other familiar humans (Horn et al., 2013). And again, like in the case of the human parent–infant bond, the quality of the bond has strong influences on all these changes just mentioned (Myers, 1984; Ainsworth, 1989).

Taken together, these findings show that dogs pay close attention, not only to the emotions and gestures of humans, but also to their actions. They even overimitate, thus showing a specific copying style that is believed to be a crucial feature of cumulative human culture. Overimitation in dogs is another strong sign for how deeply they attend to humans, especially to those with whom they have close relationships. The bond (which is selective) and the quality of the bond are of great importance for dogs' general attitude towards humans and their behavioral performance. This can be nicely seen in family dogs interacting with their caregivers. Why dogs attend so closely to the behavior of their caregivers can be explained by different reasons: they surely want to please them and are inclined to obey them. However, they might also understand themselves as partners in our social interactions and are part in our social game. Bonding and affiliation are to be understood as motivations for social interaction. Humans make ample use of the dogs' readiness to understand their actions: dogs are trained in many different ways and for many different reasons, including agility training, obedience training, and other forms of special-purpose training, in which a precise following of the trainer's behavior is the rule (Clark and Boyer, 1993).

Moral Emotions? From Biology to Philosophy

Dogs are deeply entrenched in interactions with humans, for which they are equipped with outstanding skills to understand human emotions, gestures, and actions. They form cooperative teams with us (e.g., as assistance, rescue, or herding dogs), they engage with us as communicative partners, and they have been enculturated in our society and are clearly part of our social game. Bonds between humans and dogs can be very intense and even resemble parent–infant attachment bonds. It seems to be this specific relationship of shared understanding and close affiliation that is at the heart of the view that dogs are indeed humans' best friend.

Besides the capacities we mentioned there might be other, social and cognitive abilities in dogs, some of which we do not know much about so far. Possible candidates for such capacities could be empathy, guilt, or jealousy.

Empathy can be understood, following de Waal's Russian doll model, as an umbrella term that covers all those ways in which one can be affected by others' emotions. The capacity for emotional contagion lies at its core, and outer layers of this "Russian doll" can incorporate more cognitively demanding capacities, such as theory of mind, perspective-taking, and sympathetic concern (e.g., de Waal, 2008). While the available evidence suggests that dogs are capable of emotional contagion (Sümegi et al., 2014; Yong and Ruffman, 2014; Palagi et al., 2015; Quervel-Chaumette et al., 2016; Huber et al., 2017; Bourg et al., 2020), researchers are still on the look-out for empathy-based complex behavior. First results indicate, for example, that there is "empathetically-motivated prosocial helping in dogs" and that dogs "are most likely to provide help to a human in need if they are able to focus on the human's need instead of their own personal distress" (Sanford et al., 2018, 386). However, such results stand against mixed evidence on dogs' helping behavior and against the need to clarify the underlying emotions and motivations (see e.g., Macpherson and Roberts, 2006, or the discussions in Sanford et al., 2018 and Adriaense et al., 2020). Because empathy could motivate moral behavior like helping, philosophers of animal minds and animal ethicists discuss it as a moral emotion that animals could possess (Rowlands, 2012; Monsó, 2015, 2017; Monsó et al., 2018; Benz-Schwarzburg et al., 2019).

Two other interesting candidates for moral motivations that could also shape the social interactions and relationships between dogs and humans are guilt (see e.g., Tangney et al., 2007; Prinz and Nichols, 2010) and jealousy (see e.g., Fredericks, 2012; Kristjánsson, 2015). However, the evidence here is ambiguous or non-existent. There is to our knowledge not a single paper that provides strong empirical evidence of dogs feeling guilty. On the contrary, preliminary evidence suggests that dogs are not capable of guilt, despite many owners' perception to the contrary (Horowitz, 2009; Hecht et al., 2012; Ostojić et al., 2015). Owners indeed often interpret their dogs' behavior as guilt (Hecht et al., 2012), something that can be ethically problematic: "Failure to read these gestures for what they are, or even worse, misinterpreting gestures of appeasement as a sign of the dog feeling guilty, are likely to lead to inappropriate responses on the part of the human in the situation and hence lead to escalation of the behavior resulting in lunging, snapping, and/or biting" (Mills et al., 2014). The case of jealousy is similar. We are just starting to investigate this emotion in dogs and face a limited body of research results. Interesting insights were reported by Harris and Prouvost (2014) who believe that at least some "primordial" form of jealousy, which we know from human infants, occurs in dogs as well, or from Cook et al. (2018) who investigate jealousy in dogs *via* fMRI methods. However, the results are heavily debated (see e.g., Vonk, 2018).

Interest in the named abilities in animals is rising among philosophers. This is at least partly because the presence of moral emotions in animals would mean that animals qualify as moral subjects, that is, individuals who sometimes behave on the basis of moral motivations (Rowlands, 2012). Moral emotions thus mark a minimal form of animal morality. This is ethically important. Indeed, it has been argued that minimal morality gives us a reason to owe these animals a special moral consideration, one that goes beyond the welfare approach that we so often use to evaluate our treatment of animals, be it pigs or dogs, cows, or any other non-human species (Monsó et al., 2018; Nawroth et al., 2019). If animals are moral subjects, profound ethical implications could follow, for example in the shape of animal rights (Rowlands, 2012), something we have already seen defended in ethical debates surrounding great apes (see e.g., Andrews et al., 2018). However, capacities such as empathy, guilt, or jealousy are very difficult to define conceptually (from a philosophical as well as a biological perspective). This is the case even if researchers pay much attention to them, as can be seen in the case of empathy, of which it has been said that "there are probably nearly as many definitions … as people working on the topic" (de Vignemont and Singer, 2006, 435). Adriaense et al. (2020, 62) conclude that we still face the challenge here of "closing the gap between theoretical concepts and empirical evidence." The emotions of guilt and jealousy face similar definitional problems that will surface more and more when research into them proceeds.

Research into moral emotions and other social phenomena in dogs will surely add to our understanding of their perception and behavior in the future. Perhaps we should err on the side of caution and assume that dogs are indeed moral subjects. However, based on the current state of the evidence we cannot make conclusive claims, yet. In addition, the discussion still needs conceptual input, and so we call here for interdisciplinary research on this topic. While embarking on this challenge, we should constantly re-evaluate how far our ethical thinking leads us with reference to less controversial research results, as well as maintain an open mind towards challenging inherited definitions of different capacities when there are good conceptual reasons to do so. After all, the philosophical debate on social capacities in animals increasingly leans towards de-intellectualized accounts of such abilities in animals, including moral abilities (Rowlands, 2012; Monsó, 2015) and towards an investigation into their ethical relevance (Monsó et al., 2018; Benz-Schwarzburg et al., 2019). In any case, our point in the following section is that we already face good reasons to arrive at a more profound ethical consideration of dogs than we often grant them. We will settle with the kind of ethical implications that we can derive safely by focusing on the kind of research results summarized in sections "Understanding Human Emotions: How Dogs Read Our Faces and Listen to Our Voices, Understanding Human Gestures: How Dogs Learn to Cooperate, and Understanding Human Actions: How Dogs Learn Our Social Game". We believe that the mentioned capacities suffice to argue that dogs have a profound understanding of human gestures, actions and emotions. They clearly bond with us and enter into relationships of mutual understanding and meaningful interaction. Such relationships have repeatedly been described as characterized by attachment and close bonds. Let us build an ethical argument on that.

CHARACTERIZING THE HUMAN–DOG RELATIONSHIP: ETHICAL PERSPECTIVES

Until now, we have very much emphasized a positive outlook on the human–dog relationship. It would be a one-eyed view if we would only mention the obviously positive aspects. For any ethical discussion concerning pet dogs we need to understand that, on top of the affiliative motive, the behavior of these animals vis-à-vis their caregiver is also determined by their dependency on us and thus on educational and normative influences that need to be examined carefully. In the household, humans educate the dog regarding what to do and what not to do, involving actions that are far from causally transparent, and may be purely arbitrary or – even less positively – exclusively human-centered. In dog training, for example, a precise following of the trainer's orders, commands, or behavior is the rule – and in fact expected from the dog, independently of the bonds at play, no matter what the dog's own preferences for some humans over others are, and irrespective of the dog's own intentions and desires. Are not there a lot of ethical challenges involved in the fact that dogs are so much part of the human world?

In what follows, we will engage in a brief ethical discussion of the human-dog relationship. As a necessary first step, we will characterize the human-dog relationship as one in which there is a necessary power imbalance, where one of the partners is always more powerful than the other. Following that, we will give an overview of the ethical responsibilities that arise out of this inequality when we consider it in connection to how dogs perceive us and to the pervasive influence that we can have on their character and capabilities. The owner or caregiver has certain duties, we will argue, that go beyond ensuring an adequate welfare of their pet.

The Human-Dog Relationship as a Power-Relation

Ethicists have argued that the human–dog relationship oscillates between two extremes: dogs, like other companion animals, are at the same time "pampered" and "enslaved," something that constitutes a "moral dilemma" (Irvine, 2004). "Enslaved" in this instance is to be understood as a philosophical term, coming from an ethical approach that departs from the fact that companion animals exist for human purposes and are defined by the law as our property (Irvine, 2004, 5). We can add aspects of dominance, ranging from a restriction in personal freedom (covering all aspects of a dog's life, like feeding regimes, mating choices, or neutering policies) to forms of labor (like the use of dogs as sheep-herding, guiding, sniffing or rescuing staff). Most importantly, it is questionable whether dogs give in any form their free and informed consent to fulfill the tasks we assign to them. Dogs are clearly capable of cooperating with humans (skills-wise) and often happily seem to do so. But freedom (even in a minimal sense) is about opportunities and choices, and how much of these do they have? As we are talking about an animal that is very much dependent on her caregiver's choices and who is being purposefully bred as well as (often quite heavily) trained to fulfill certain human-oriented tasks, the question seems warranted (Cochrane, 2009, 2012; Schmidt, 2015).

Thereby, it seems possible, and even morally desirable, to grant an animal more choices and thus more freedom. Yeates (2015, 168) identifies a range of situations where we should from a normative perspective respect the animal's choice. These are for example situations in which we ourselves lack "accurate knowledge of the animal's subjective experiences," or in which we do "not know what will lead to desirable experiences or allow for the avoidance of undesirable ones," when we are "biased" or "less aware of the animal's specific situation." He argues, furthermore, that we should better turn to respect the animal's choice when we ourselves "cannot appreciate all elements comprehensively, including considering any value to the animal being allowed to make and implement a choice, such as where a lack of control or liberty would be unpleasant or where an animal would usefully learn from the process of choice-making." Such an approach ultimately aims to reduce the power hierarchy and "set up situations that empower animals" to make their own choices.

Up to now, the high amount of paternalism and training involved in the human–dog relationship gives rise to a clear power relation. For sure, more and more trainers adopt training methods that turn away from a behavioristic understanding and work in a scientifically informed manner. But the many different perspectives on suitable training methods and the many noncertified methods and noncertified institutions in the dog training business lead to much diversity in the field. Thus, even though the field has moved forward in the past few years, it seems difficult to assess how scientifically informed the majority of trainers (let alone owners) actually treats and trains their dogs. Also, some dog trainers with massive public outreach even add on the mentioned questionable understanding by arguing that all dog training is ultimately about teaching the dog that the human is pack leader. Cesar Milan, one of the most influential and controversial dog trainers, describes "Pack Leadership" as a core principle of his training strategy, to be applied in the following way: "Establish your position as pack leader by asking your dog to work. Take him on a walk before you feed him. And just as you do not give affection unless your dog is in a calm-submissive state, do not give food until your dog acts calm and submissive" (Milan, 2019). Still, even without such an idea of discipline and submission, other forms of dog training based on purely positive reinforcement also resort to methods that heavily impact on the dog's will, her choices, preferences, and intentions. Some methods tie almost all feeding to training steps by reinforcing every positive behavior with food, sometimes while putting the dog otherwise on food deprivation. Lindsay describes in his *Handbook of Applied Dog Behavior and Training* that training only works if the animal is "in a state of need" that can be satisfied only after the dog behaves in a "predetermined way." Therefore, "combining food deprivation together with the presentation of special treats produces the best training results. The term deprivation means scheduling training sessions before meals rather than after them. The meal itself can be given to reinforce the overall training session as a sort of jackpot" (Lindsay, 2000, 249).

We have come across a substantial reinterpretation of affection as something that is not given to the dog "unless the dog is in a calm-submissive state" in Milan's (2019) training procedure and another substantial reinterpretation of feeding the dog in the sense that meals become a "sort of jackpot" in classical, modern reinforcement training. These narratives are normatively relevant because they show the tight entanglement of power, predetermination, and submission in dog training, expressed by a language in which dogs "work" for us. No matter the method, all training ultimately educates the dogs into a human world with the aim that they function properly, that is, according to valued and dis-valued behavior in this setting: they are not supposed to chew on our furniture, pee on our carpet, or chase the neighbor's cat. Spaces where a dog can, for example, run free without a muzzle or leash and interact with other dogs are clearly restricted as well as rare, at least in urban settings, where numbers of dogs have been increasing dramatically over the past decades, standing currently at well over 60 million in the United States alone (American Pet Products Manufacturers Association, 2020).

We are aware that this understanding draws a rather sobering picture of the often romanticized human-dog relationship. However, pet keeping is not a given or simply a result of a natural affinity between humans and animals. It is a historically contingent practice that has also been circumscribed by social class and gender constructs (Irvine, 2004, 19). This is a sociological point that links with ethical and biological perspectives: like all our relationships with companion animals, the human-dog relationship depends on how we define animals, and for that our knowledge about their abilities and needs seems crucial. For sure, it is also crucial how ready we are to take their perspective into consideration. For this, questions of power and hierarchy are relevant.

So let us start from the premise that the human-dog relationship can be described as a human-dominated power relation in which dogs often have little choices and humans perceive themselves on a spectrum between guardians and leader of the pack. Given this power relation at place, and given a generalized lack of awareness of the latest research on dog social cognition, humans tend to interpret communicational misunderstandings as problems of the dog (e.g., in the sense of non-obedience). They consequently tend to interpret the behavioral reactions of the dog to such miscommunication not as a result of miscommunication (for which they themselves are also co-responsible) but again as a problem of the dog, who is, for example, claimed to be aggressive. Humans need to take responsibility here. We are left with the necessity to better understand how dogs perceive us and what they are capable of. Our summary of the socio-cognitive abilities of dogs only shows the tip of the iceberg of what these animals can do. We should not forget that they are quite different from ourselves with respect to their perceptual repertoire: humans, other than dogs,[3] rely much more on vision, are relatively insensitive to odors, and so forth. Taking our visual perceptions, our facial expressions, and our emotions and actions into account to the extent dogs obviously do, renders their social life rather complicated. Living in a human's world can thus be very demanding for dogs and some dogs might be overwhelmed. It is our responsibility to gain awareness of the challenges we face them with.

In addition, we need to deepen our understanding of the kind of relationship we offer them and the power relations characterizing it. Here too, gaining awareness means shifting the focus from the dog to the human, and consequently taking responsibility. We need to arrive at a better understanding of the range of concrete duties dog owners have. In what follows, we will argue that humans are to a large degree responsible for who their dog turns out to be and that they have a duty to ensure her adequate flourishing. Not only this, the characteristics of the human-dog relationship point to a propensity towards trust on behalf of the dog, and consequently entail a duty not to betray that trust.

The Duties of Dog Caregivers

In animal ethics, there is a generalized agreement that humans have negative duties towards (at least some) animals. Negative duties refer to duties not to cause unjustified harm, a position that can be defended from a number of ethical theories, including utilitarianism (Singer, 2009), deontology (Regan, 2004), and virtue ethics (Hursthouse, 2011). However, negative duties do not exhaust all that morality demands from us. In human-human relationships, we are also often required to assist someone in need, even if we are not responsible for their harm. For instance, if we witness someone falling onto the train tracks at an underground station, we are morally required to do our best to save them, even though their peril is not our own fault. These are known as positive duties. In those cases, in which there is a pre-existing special relationship, these positive duties are even stronger. Parents are not only required not to harm their children and to assist them when they are in need, they are also required to do all that is in their power to ensure that they have a good life. This means providing them with food and healthcare, but also ensuring that they receive a proper education, that they have opportunities for exercising their creativity and making friends, that they feel loved and cared for, and so on. In short, that they flourish as the sort of beings they are. Rowlands (2012) considers that this treatment is owed as a matter of respect: "to respect an individual is, fundamentally, to respect it as the kind of individual it is" (Rowlands, 2012, 249). If, indeed, the dog-human relationship entails forms of attachment that resemble our bonds with human children, the question then arises: what would respecting our dogs as the kinds of beings they are look like?

Palmer (2010) has argued that when considering the duties that we owe to other animals, we cannot follow a one-size-fits-all logic, even in those cases where different species have similar cognitive capacities. She argues that the surrounding context, the history, and the pre-existing relation are fundamental in determining the kinds of duties that we owe to a particular animal. With regards to those animals who live independently from us in the wild, we only have negative duties not to harm them. In contrast, those animals with whom we have some sort of special relationship will, in addition, generate positive duties. If we consider the case of dogs, this is clearly going to be one of the most demanding human–animal relations from a moral perspective. As we have already discussed, dogs

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[3] Dog's sensitivity to odors allows humans to train them as sniffer dogs for all sorts of purposes, from finding substances, like marihuana or explosives, to discovering injured persons after earthquakes, from detecting illnesses, like cancer, to helping out in species conservation (see Fischer-Tenhagen et al., 2017).

are the oldest domesticated species. This history has generated a very high degree of vulnerability and dependency in those dogs that live in our households. They depend on us for food, shelter, and medical care. Indeed, they depend on us for sheer survival. As we have seen, dogs also have a highly malleable nature and we can shape their character to a large degree. Dogs play very little part in choosing their caregiver, and still the person they end up with will have a profound influence on their life and on the sort of individual they turn out to be. So, they also depend on us to a much deeper level. This, coupled with the aforementioned power relation, generates positive duties that go beyond simply ensuring that the dogs in our household have a good welfare.

We are responsible for our dogs' lives from beginning to end, and this means that we will have an immense causal influence on the quality that their life ultimately has. This generates a duty to ensure that our dogs lead a good life. But what does it mean for a life to be good? Different philosophical traditions have offered different answers to this question (for an overview of these different theories see Crisp, 2017). From the perspective of a common theory known as hedonism, a good life is one in which there is, overall, more positive subjective experiences than negative subjective experiences. For a dog this might mean a life in which she is in general happy and has very few painful or fearful experiences. From the perspective of desire-satisfaction theories, in contrast, a life is good if the individual's most important desires are fulfilled. For a dog, this could mean a life in which she gets to do all the things that she really cares about. We believe that neither of these two options gives a satisfactory account of what it would mean for a dog to have a good life.

It is easy to see why the desire-satisfaction account of a good life is not adequate, at least in the case of dogs. This is due to the mismatch between their biological roots as wolves and the fact that they have been domesticated. This history has led to a situation in which, firstly, not all the desires that dogs have are actually good for them. For instance, many dogs, if let by their caregivers, will eat much more than they actually need, and consequently develop different health problems in the long run. The tendency to eat more than needed might be good for a carnivore who lives in the wild and does not get to eat very often, but for a pet in a household with unlimited access to food, it can significantly worsen her quality of life. Secondly, it is not just important to determine what dogs desire, but also what are the reasons behind those desires. As we saw before, dogs are very often eager to cooperate with humans, but it is difficult to see what the exact motivation behind this eagerness is: Is it the expectation of a reward? Is it fear of punishment?, or Is it a desire to please the caregiver or a desire to be part of the social game? The history of domestication has also led to dogs being shaped to be eager to cooperate with us. In this sense, many of their desires are the result of a process of selective breeding that could be comparable to a process of indoctrination in humans. Therefore, from the fact that a dog has a desire, the conclusion that it is good to satisfy this desire does not automatically follow.

Desire-satisfaction theories thus cannot provide us with a satisfactory account of what it means for a dog to lead a good life. But what about hedonism? Surely a life in which a dog is overall happy is a good life for that dog? We believe that hedonism, just like desire-satisfaction theories, captures an important aspect of what it means to lead a good life, but cannot give us the full story. In philosophical terms, having more positive than negative subjective experiences throughout one's lifetime is a necessary but not sufficient condition for a good life. Imagine a dog, we can call her Frida, whose caregiver decides to keep her inside the house her whole life to protect her from possible dangers and fearful stimuli she might encounter outside. Frida is provided with an adequate diet, a comfortable bed in which she can rest, and enough toys to keep her entertained. The extremely controlled environment she is kept in ensures that she very rarely experiences any accidents or illnesses, stress or pain. If we look at Frida's life as a whole, we will see that she is extremely pampered, to say it in Irvine's words, and overall happy. But is this a good life?

We believe that Frida's life, while certainly far from terrible, is not a good life. This has to do with the fact that, by not being allowed to encounter challenges, to interact with con- and heterospecifics, and to explore the outside world, Frida is prevented from flourishing as the type of being that she is. As we saw in the previous sections, dogs have many amazing socio-cognitive skills but these are largely dependent on how we have shaped them during domestication and what they learn from interactions with humans during ontogeny. We believe that caregivers have a positive duty to ensure that these capabilities can develop, not only so that the animals can better cope with the challenges they might encounter in their lives, but also because it is a good thing for them to be allowed to flourish as the type of being they are, an idea that can be captured, for instance, using the capabilities approach (Nussbaum, 2007; Monsó et al., 2018).[4] Allowing for the dogs in our care to develop their socio-cognitive skills also enables them to have a life that is more meaningful. According to Purves and Delon (2018), animals' lives acquire meaning when they are allowed to exercise their agency and use it to bring valuable states of affairs to the world. These valuable states of affairs range from relatively simple endeavors like rearing their young or establishing friendships, to more demanding behaviors like rescuing a human in need (which recent research shows dogs are capable of; Bourg et al., 2020). A dog who is allowed to flourish to her full capacity is more likely to lead a meaningful life, which will in turn be a better life.

In addition to the duty to ensure the flourishing of the dogs under our care, there is also an additional duty that emerges from the special relationship that we have towards

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[4] One could object that the fact that dogs share an environment with us gives us a reason to restrict their freedom. However, it is important to remember that dogs did not choose to share an environment with us. If we were to hold a human captive in our household, it would surely be very problematic to claim that this 'shared environment' gives us a reason to restrict her freedom. On the contrary, the existence of a shared environment gives us a reason to respect others' freedom and interests, as has been long defended within social contract theory.

dogs, and from the specific way in which dogs perceive us. In our review of the empirical evidence regarding dogs' perception of humans, we have highlighted the special characteristics of the dog–human bond. Dogs are not only eager to cooperate with us; they are also attuned to us like no other species. Their tendency to overimitate humans, for instance, points to a perception of us as important social partners. We know that dogs can recognize individual humans and they are also significantly less fearful of us than are their wild ancestors. All of this points to the ease with which a relationship of trust among dogs and their caregivers can emerge. Placing your trust in another allows for significant social bonds to be built, but it also means that one is made more vulnerable. The moral importance of this was captured by Cooke, who wrote that "[i]n trusting another, we give them power over us, power to set back our projects, exploit us, and make us vulnerable not just to them, but to others also" (Cooke, 2019, 188)[5]. The trust that dogs place in us is no coincidence; instead it is a result of the process of domestication of which we are at least partly responsible as well as a result of what they learn in interactions with us during their lives. Humans thus have a duty to live up to this trust (see similarly Hens, 2008), to ensure that our dogs' needs are met, and that they are not placed in a situation where it would be warranted for them to feel betrayed. To paraphrase Cooke (2019, 198), humans have a duty to act in ways that make them worthy of the trust that dogs place in them. For this duty to exist, it is not necessary for dogs to possess a cognitively complex form of trust for which we do not have any empirical evidence, yet. Our argument is that the way dogs engage with us evidences a trusting relationship that gives rise to duties on our side (not on theirs). For the kind of trust we are after we do not need the dog as a moral agent to fully understand what trust is in a normative sense, nor do we need the dog to understand duties on her side. Dogs' capacity to enter into such relationships with us is independent of the question of whether they have (in addition) the sort of capacity for full-blown moral judgment that orthodox frameworks of moral agency require, or even a simple explicit motivation to trust their owner (which could make them a moral subject in Rowland's sense). At least the former, intellectually demanding forms of trust might be tied to other complex abilities, such as a theory of mind. Our point is humbler here but still of profound relevance: the kind of trust we identify in the human-dog relationship becomes an ethical signpost in the light of the dog's dependency on her caretaker.

CONCLUSION

Dogs have indeed special skills to understand and interact with humans due to the evolutionary history and domestication of the species and due to complex competences acquired by individual and social learning. We see accumulating evidence of their understanding of human emotions, gestures, and actions and of how much they are thus part of human culture and our social game. Bonds between dogs and humans are selective, intense, and vary in quality. Affiliation plays a motivational role in dog behavior and shapes the dogs' attitudes as well as their interaction with humans. All of this, however, has to be seen in the light of a comprehensive characterization of the human-dog relationship, which is a socially constructed practice with clear power relations. We have argued that the human-dog relationship is a dominance relationship where humans are usually in command of power. If caregivers are unaware about how much their dogs pay attention to subtle communicative cues and how much they understand about as well as attend to their caregivers' emotions, gestures, and actions, a range of conflicts can arise. Instead we should invest into building relationships of trust with dogs that live up to ideas of companionship.

Irvine (2004) arrived at the conclusion that "relationships between humans and animals have depended on how a given society defines animals and what it means to associate with them". She argues that "what we currently know about animals demands wrestling with the moral implications of keeping them as pets" (Irvine, 2004, 5). We have been following this critical view of pet keeping in general and dog keeping in specific, because it could serve as a helpful heuristic to map out problems that are often overlooked, specifically problems that point beyond welfare towards other normative concepts. Sixteen years after Irvine's paper we face a substantial amount of new research results on dog social cognition which we have summarized in this paper and which we need to take into account when debating the human-dog relationship today.

From what we have discussed we gain a better understanding of a main characteristic of the human-dog relationship that lies in its dichotomy between special attachment as well as special understanding on the one hand and the instrumentalization of dogs on the other hand. Against this backdrop, a meaningful social interaction between dogs and caregivers remains a fragile construct. In order to treat dogs in the way that morality requires of us, it is paramount that we bear in mind the spectrum of positive duties that this relationship engenders, including the duty to live up to the trust that dogs place in us.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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[5] Note that Cooke's theory does not require any sort of cognitive notion of trust as a capacity dogs have. Instead, we would argue, trust emerges as a disposition in dogs, as a result of their phylogenetic and ontogenetic makeup and it is necessary to enter into a relationship of mutual understanding and social dependency.

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The Gaze Communications Between Dogs/Cats and Humans: Recent Research Review and Future Directions

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Dogs (*Canis familiaris*) and cats (*Felis silvestris catus*) have been domesticated through different processes. Dogs were the first domesticated animals, cooperating with humans by hunting and guarding. In contrast, cats were domesticated as predators of rodents and lived near human habitations when humans began to settle and farm. Although the domestication of dogs followed a different path from that of cats, and they have ancestors of a different nature, both have been broadly integrated into—and profoundly impacted—human society. The coexistence between dogs/cats and humans is based on non-verbal communication. This review focuses on "gaze," which is an important signal for humans and describes the communicative function of dogs' and cats' eye-gaze behavior with humans. We discuss how the function of the gaze goes beyond communication to mutual emotional connection, namely "bond" formation. Finally, we present a research approach to multimodal interactions between dogs/cats and humans that participate in communication and bond formation.

Keywords: dogs, cats, humans, gaze, interaction, communication, bond

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DOMESTICATION OF DOGS AND CATS

Dogs (*Canis familiaris*) and cats (*Felis silvestris catus*) are the closest animals living with humans. Dogs, domesticated approximately 15,000 years ago, were the first animals domesticated from wild species (Freedman and Wayne, 2017). They acquired social tolerance to humans and cooperated with humans by assisting in hunting and guarding. Dogs were first selected because of their reduced stress response to humans, and then for the usefulness of their cooperation with humans (Driscoll et al., 2009). Wolves (*Canis lupus*), sharing a common ancestor with dogs, have developed a greater ability to cooperate than dogs, but wolves only display intra-specific cooperation. In contrast, cats were domesticated approximately 10,000 years ago, primarily because they were predators whose prey included rodents (Vigne et al., 2004). Additionally, cats were not artificially selectively bred. The cat's ancestor is the wildcat (*Felis silvestris lybica*), a solitary, territorial animal, like most other Felidae (Bradshaw, 2016).

Although dogs have ancestors with a different nature than cats, and were domesticated via different processes, they are the most common animals living with humans (**Figure 1**). The foundation of this coexistence is non-verbal communication. They use their sense of smell, hearing, touch, and eyesight to communicate with humans. Dogs and cats are sensitive to gaze, which humans use as a form of non-verbal communication. In this review, we introduce the communicative function of gaze in dog-human and cat-human interactions in recent studies (**Table 1**). Second, we describe bond formation beyond communication and the importance of gaze in bond formation. Finally, we discuss the possibility that other senses contributed to the bonds formed between dogs/cats and humans and a research approach to the multimodal interactions that facilitate communication and bond formation. Comparing the ways dogs and cats interact with humans provides insight into how both species have integrated into human society. In other words, the differences between dogs and cats may have originated due to differences in their ancestral species' social natures and the process of domestication. The similarities between dogs and cats may also be due to changes in their cognitive function that allowed them to integrate into human society. With these considerations in mind, we review the findings to date.

GAZE COMMUNICATION FOR DOGS

It is easy to determine the direction of gaze of wolves that hunt cooperatively in packs because of the type of eyes they have. Furthermore, wolves have developed behaviors for receiving and sending their gaze signals (Ueda et al., 2014). These results suggest that wolves use gaze to communicate with others. It is possible that dog's ancestors inherited this function and dogs have applied it as gaze-based communication in their interactions with humans.

When dogs receive human gaze, they change their behavior depending on its direction. For example, dogs were given a series of trials in which they were forbidden to consume any visible food (Call et al., 2003; Kaminski et al., 2013). When the human looked at them, dogs retrieved food less often than in the conditions in which humans did not look at them. Additionally, dogs were more obedient to their owners' commands when their owners looked at them (Schwab and Huber, 2006). Dogs detect a human's attentional state from the direction of their gaze. This behavior is necessary for dogs' ability to respond to human commands, such as when hunting. Furthermore, dogs expect what humans can see and change their behavior accordingly. For example, in an experiment, two toys were placed in a room, one was blocked by opaque panels to prevent humans from seeing it. Although the dogs could see both toys, when ordered to "fetch," they picked the one visible to the humans (Call et al., 2003). In another experiment observing the free behaviors of dogs, the duration of their attention-getting behaviors (e.g., whining, whimpering, and looking at owners' faces) was longer in response to their owner's gaze (Ohkita et al., 2016). This ability to recognize other's perspectives could be beneficial to humans' and dogs' cooperative hunting.

Dogs are more likely to select food from humans who are looking at them than those who are not (Gácsi et al., 2004); this tendency was likely to have been acquired early in the domestication process. Dogs often exhibit more hesitative behaviors when approaching a blindfolded human but beg for food from a human with visible eyes (Gácsi et al., 2004). This difference indicates that, based on gaze, dogs may distinguish between humans who are willing to give food and those who are not, and they receive food from the former when they are allowed to consume. Food, and knowing if someone would give them food, was a significant factor in dogs' early domestication.

Dogs use human signals such as pointing (Miklosi et al., 2005) and gazing accompanied by pointing even when they are puppies (Hare et al., 2002). One study showed that dogs were easily able to use human pointing to select one of two containers in which food was hidden using human pointing and gaze direction. In contrast, chimpanzees, close relatives of humans, find it difficult to use human cues in this task. Furthermore, a dog's gaze follows only a human gaze (Hare et al., 1998; Agnetta et al., 2000; Téglás et al., 2012; Met et al., 2014). They look in the direction in which the human gaze (with head movements) is directed. Dogs follow not only the gaze but also the movements of humans. When there were two bowls with food, dogs followed the one that more humans went to under certain conditions (Nagasawa et al., 2020). Dogs chose the same container they had seen humans choose, even if they had seen the human removing food from it and pretending to eat it (Chijiiwa et al., 2020). Following human behaviors, including gaze, would have helped dogs-human cooperation for hunting and gathering before humans began establishing cultures based on cultivation and settlements.

Dogs exhibit social referencing by looking at and using facial expressions and behaviors of others in unfamiliar situations. In unsolvable tasks in which they cannot access food, they look at their owners (Miklosi et al., 2005), but see Lazzaroni et al. (2020). Even when they encounter a strange object, a fan with some ribbons, most dogs look referentially to their owners after looking at the strange object (Merola et al., 2012a,b). This alternating gaze is thought to have the function of joint attention, directing others' gaze to an object to garner problem-solving cooperation. In humans, alternating gaze followed by joint attention is thought to be related to identifying intention and establishing reference (Emery, 2000). Dogs can also use their own gaze to guide a human's gaze. Although the function of dogs' alternating gaze from objects to humans is unclear, dogs may rely on humans to help them in situations where they did not know what to do or cannot solve problems themselves.

Recent research suggests that dogs' gazing behaviors with humans are influenced by the dogs' life experiences (Marshall-Pescini et al., 2017; Brubaker et al., 2019). Hence, both domestication and socialization influence a dogs' gaze behavior with humans.

GAZE COMMUNICATION FOR CATS

The ancestors of cats lived alone; therefore, they may not have needed the ability to read the gaze of other individuals as much as species that hunted in groups. However, there are some recent reports of communication through gaze between cats and humans.

Cats detect human gaze with head movements and accordingly change their behavior (Koyasu and Nagasawa, 2019). When a familiar human (i.e., experimenter) and a cat spent time in the same room, the cat's behavior was observed in response to the familiar human's gaze. Cats looked at a familiar human for a shorter duration when the cats were directed gaze than when the cats were not, suggesting that, unlike dogs, they exhibit the behavior of avoiding a familiar gaze. Cats may see a human gaze

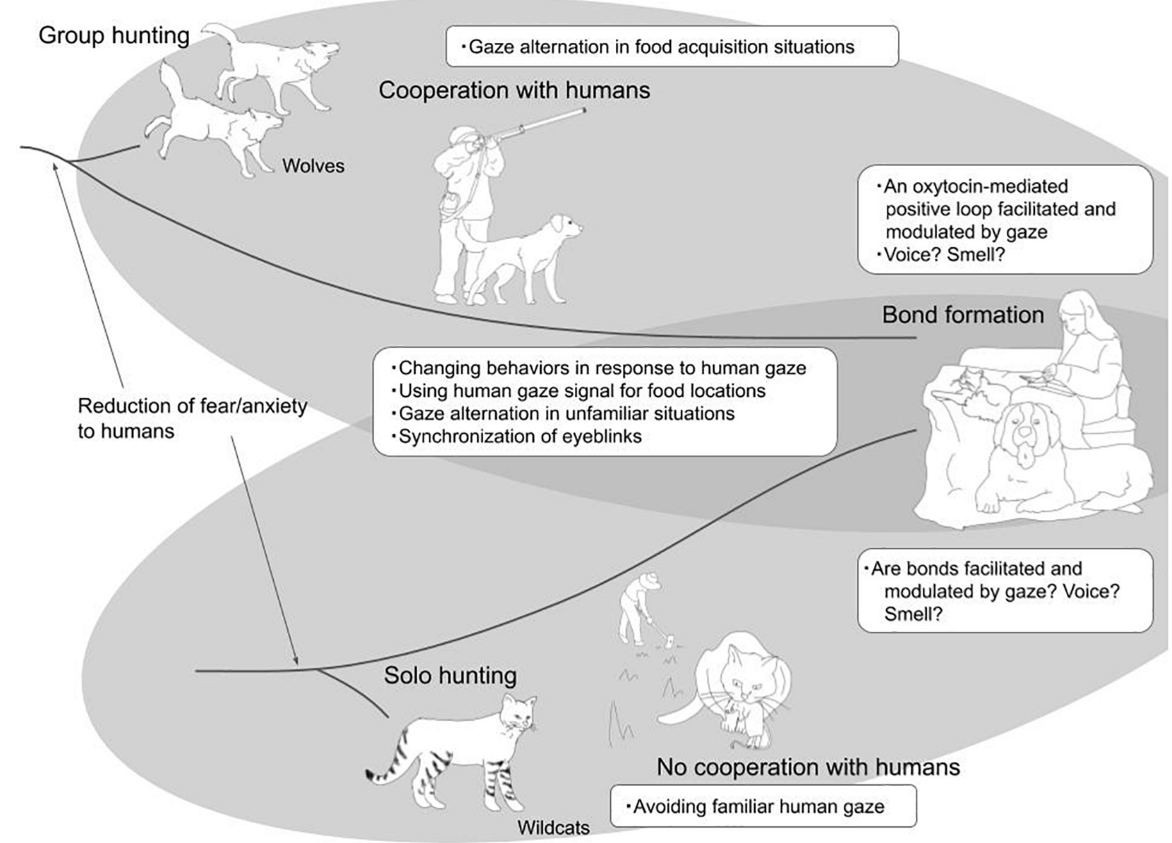

FIGURE 1 | Domestication of dogs and cats and gaze communication with humans. Although dogs and cats have ancestors with a different nature, they have started living with humans, using nonverbal communication, especially gaze. The similar gaze communications observed in both dogs and cats were shown in the overlap of two circles. Using non-verbal communicative signals they can form bonds with humans.

as the same thing as a cat's gaze, which indicates a threat in a social situation with no goal or threat (Bradshaw, 2016).

However, in a study with feeding situations, cats were fed by humans who gazed at them (Ito et al., 2016). As with Gácsi et al. (2004), two humans performed differently in front of cats. Cats selected more food from humans who called their names with gazing than food from humans who called their names without gazing. Whether or not cats avoid/select gaze may depend on the experimental situation. Cats also use human signals (Miklosi et al., 2005). Regarding the ability to use human pointing, no statistically significant performance has been found between dogs and cats.

Furthermore, cats can follow a human's gaze (Pongrácz et al., 2019). In a two-way food selection situation, cats followed a human gaze (with a head movement) in about 70% of the trials. In the condition for selecting one of two food bowls, cats also followed the movements of humans, not just their gaze. As with dogs, cats visited the container following humans, even after seeing the human removing food and pretending to eat it (Chijiiwa et al., 2020). As cats became a part of human society to catch mice but were not required to serve any other role, they may have acquired these abilities in their development because of their dependence on humans for food today. These similarities between dogs and cats indicate they are both easily affected by human behaviors in situations involving food, despite the two species' different domestication histories.

Cats did not exhibit social reference behavior in the unsolvable task in a feeding situation, unlike dogs (Miklosi et al., 2005). Cats may use the cues provided but not demand cues themselves. Because they did not rely on others for food, they do not demand cues themselves. However, depending on the situation, cats do exhibit social reference (Merola et al., 2015). When cats were shown the fan with some ribbons, 80% alternated their gaze between the fan and their owner, but their behaviors changed based on the human's emotional expression. When cats encounter strange objects and do not know what to do, they can read the human's facial expression/behavior or lead the human gaze to objects. Considering the process of domestication, these results may be due to cats' lack of a history of cooperating with humans to acquire food.

Thus, cats avoid/select the gaze and exhibit/do not exhibit social references depending on the social context. Investigating the contexts in which they require a human gaze may clarify the factors that facilitate the acquisition of human-like communication skills, but cats undoubtedly use gaze to communicate with humans. It is considered to have evolved through life with humans, although the gaze function originally was not necessary for cats.

TABLE 1 | Gaze communication between dogs/cats and humans.

Dogs	References	Cats	References
Response to human gaze			
Stole food less often	Call et al., 2003; Kaminski et al., 2013	Avoided the gaze of familiar human	Koyasu and Nagasawa, 2019
Obeyed more commands of their owners	Schwab and Huber, 2006	Selected food from humans who looked at them	Ito et al., 2016
Fetched the toy that humans could see in the situation with two toys	Call et al., 2003		
Increased attention-getting behaviors	Ohkita et al., 2016		
Selected food from humans who looked at them	Gácsi et al., 2004		
Using human signals			
Used human pointing in the task of selecting one of two containers	Miklosi et al., 2005	Used human pointing in the task of selecting one of two containers	Miklosi et al., 2005
Used human gaze direction with pointing in the task of selecting one of two containers	Hare et al., 2002	Looked in the direction indicated by human gaze (with head movements)	Pongrácz et al., 2019
Looked in the direction directed by human gaze (with head movements)	Hare et al., 1998; Agnetta et al., 2000; Téglás et al., 2012; Met et al., 2014	Followed the container that humans visited in a situation with two food containers	Chijiiwa et al., 2020
Followed the container that humans visited in a situation with two food containers	Chijiiwa et al., 2020; Nagasawa et al., 2020		
Social reference			
Looked alternately at the food and the owner when it could access the food	Miklosi et al., 2005, Lazzaroni et al., 2020	Did not look alternately at the food and the owner when it could not access the food	Miklosi et al., 2005
Looked alternately at the strange object and the owner	Merola et al., 2012a,b	Looked alternately at the strange object and the owner	Merola et al., 2015
The role of gaze in bond formation			
Increased attention-getting behaviors in dogs, which function as attachment behaviors in response to human gaze	Ohkita et al., 2016	Eyeblink synchronization during mutual gazing	Koyasu et al., 2020
Dog owner's oxytocin secretion increased in response to the dog's gaze	Nagasawa et al., 2009		
An oxytocin-mediated positive loop of bond formation facilitated and modulated by gazing, like mother-infant	Nagasawa et al., 2015		
Eyeblink synchronization during mutual gazing	Koyasu et al., 2020		

BOND FORMATION BETWEEN DOGS/CATS AND HUMANS

Dogs/cats can distinguish between signals based on human emotions. Dogs change their behavior depending on the emotional state of humans. In one study, dogs sniffed, nuzzled, and licked a human who was pretending to cry (Custance and Mayer, 2012). In the social referencing experiment described above, dogs approached the strange fan when their owners reacted positively and moved away from it when their owners reacted negatively (Merola et al., 2012b). Dogs also distinguished between emotional states and facial expressions of humans (Nagasawa et al., 2011; Buttelmann and Tomasello, 2013; Turcsán et al., 2015). Likewise, cats change their behavior depending on the human emotional state. When an owner was depressed, the cat rubbed against their owner more often (Rieger and Turner, 1999). A study showed that a cat's behavior toward its owner during interactions was affected by their owner's emotional state (Turner and Rieger, 2001). As with dogs, they distinguished between humans' facial expressions and associated postures (Merola et al., 2015; Galvan and Vonk, 2016) and strangers' voices (Quaranta et al., 2020). Dogs/cats can distinguish between signals based on human emotions, which would be the foundation for forming emotional bonds.

Previous studies also suggest that emotional bonds exist between dogs/cats and humans. To examine whether an emotional bond is formed, it is necessary to know if animals show 1) an emotional or behavioral response to specific individuals and 2) a stress response to separation and a stress reduction/pleasurable behavior in reunions (DeVries, 2002). The Ainsworth Strange Situation Test (SST) has been widely used to demonstrate infants', dogs', and cats' bonds to their primary caretakers.

In novel environments, dogs' exploring and playing behaviors increased when there was an owner in the room compared to when there was only a stranger in the room, and their following behavior increased when the owner left the room compared to when the stranger left the room (Topal et al., 1998). This observation means that dogs behave differently toward their owners than strangers; their owners function as a secure base, like the human mother-infant bond.

In the formation of these human-dog bonds, gaze plays an important role. In experiments observing the free behaviors of dogs in response to human gaze, dogs' attention-gaining behaviors increased when owners looked at them (Hare et al., 2002). Dogs' increased attention-seeking when receiving a human gaze may be an attachment signal to draw their owners to them. Furthermore, the dogs' gaze directed at their owners led to increased oxytocin secretion in their owners (Nagasawa et al., 2009). The oxytocin neuroendocrine system is associated with uterine contraction during childbirth and the promotion of breast milk secretion and plays an important role in maternal behaviors following birth (Nagasawa et al., 2012). A dog's gaze increased the owner's interaction with the dog, which increased oxytocin secretion in dogs; in other words, there is an oxytocin-mediated positive loop of bond formation facilitated and modulated by gazing in human-dogs, like mother-infants (Nagasawa et al., 2015).

Cat-owner bonds are a form of attachment similar to that between dogs or infants and their caretakers (Edwards et al., 2007). In the SST, cats have been shown to spend more time engaged in locomotion/exploration when accompanied by their owners and exhibited higher alert behavior event frequency when accompanied by strangers. In a study reexamining these bonds using a crossover design experiment with an improved and counterbalanced modification of the SST, cats vocalized more when owners left the room than when strangers left (but there was no other evidence of a secure base) (Potter and Mills, 2015). Recently, a secure base test (SBT) was conducted to investigate whether humans function as an attachment figure for cats (Nagasawa et al., 2009). The cat-human bond was found to be similar to mother-infant and dog-human bonds; however, additional experimentation with strangers is required due to the lack of evidence that the bond was to a specific individual. There was proximity seeking, separation distress, and reunion behavior, which are indicators of attachment relationships between cats and caretakers. As shown, there is some evidence that there are cat-human bonds. However, it is unclear whether gaze facilitates the bond formation, as in a dog-human relationship. Since cats also communicate through gaze, especially with humans, gaze may be an important factor in bond formation.

Eyeblink, an unconscious signal, may also play a role in the mutual gaze that facilitates bond formation. A study reported that during mutual gaze, eyeblinks were synchronized between dogs and humans (Koyasu et al., 2020). Dogs blinked about one second after their owner or a stranger blinked. The owners blinked immediately after the dogs had blinked, and the strangers blinked after some delay following the dogs' blinks. Although there was some time lag, the presence of mutual blink synchronization was suggested. The same phenomenon was observed in cats. This synchronization is considered to lead to a mutual understanding and effective communication in humans. Synchronizing and obtaining the same physiological state as others may also lead to mutual understanding and effective communication in dogs and cats.

These results suggest that a similar communication signal evolved in humans, dogs, and cats. However, individual differences—specifically in personalities—exist. As dogs/cats and humans spend time together in a house, they can learn communications unique to the pair/group and probably form bonds with specific individuals. The bonds would be more beneficial for dogs and cats in terms of leading to more food, better food, and greater safety, and more beneficial for humans in terms of being less stressed, less anxious, and healthier. Therefore, interspecific bonding benefits both parties.

VOICES AND SMELL THAT MAY CONTRIBUTE TO BOND FORMATION

Since dogs and cats discriminate between humans using integrated different types of senses, other senses, such as auditory and olfactory, may also contribute to bond formation. Along with visual information, other forms of perceptual information may promote bond formation. Cats have adapted their voices to communicate more effectively with humans. For example, adult cats meow at humans (Mertens and Turner, 1988), but otherwise, meowing is generally only used for communication between kittens and their mothers (Bradshaw and Cameron-Beaumont, 2000). Additionally, domestic cats' meows are more comforting to humans than those of wildcats (Nicastro, 2004), and feral cats' meows are different from house cats' in acoustic variables indicated by a spectrogram (Yeon et al., 2011). Another example is that cats purr more when they are reunited with their owners after a long separation (Eriksson et al., 2017). Purring is a general sign of contentment or care soliciting behavior (McComb et al., 2009). Although purring can occur in different contexts (Merola and Mills, 2016), it is most commonly seen in kittens to solicit care from mothers (Bradshaw and Cameron-Beaumont, 2000). It is considered that domestication and socialization have led to the development of a cat's vocal communication with humans. Cats are also sensitive to human vocalizations. Cats distinguish between the voices of their owners and strangers (Saito and Shinozuka, 2013). Cats participating in a habituation-dishabituation test showed a decreasing response when strangers' voices continued and increasing head and ear movements when hearing their owner's voice. Dogs also distinguish the voices of their owners (Adachi et al., 2007) and read human emotions through voice and intonation (Andics et al., 2016).

Cats also have highly developed communication through smell. Most small felids, including *Felis silvestris lybica,* the ancestor of cats, have exclusive territories. Species with large territories rarely encounter others and tend to communicate through smell. Some cats live in multi-cat households and high-density urban environments. Cats living in groups may distinguish between individuals who are group members and non-group members through smell. Cross infection between individuals during allorubbing or while marking communal scent posts would increase any similarity of smell profiles among the members of a social group, but that is not conclusively demonstrated (Gittleman, 2013). Thus, communication through smell in cats may be more complex than in other felids. They also communicate with humans through smell, as they exhibit rubbing behavior. The connection between their rubbing and social bonding is supported by the fact that cats are adept at communicating through smell. Smell helps dogs distinguish between their owners and strangers. The caudate nucleus region of dogs' brains is more strongly activated when exposed to familiar human smell compared to the smell of familiar dogs, unfamiliar dogs, unfamiliar humans, and their own smell, suggesting a positive emotional response to familiar human smell (Berns et al., 2015). Dogs may also distinguish human emotions by smell. Dogs showed higher cardiac activation when sniffing human fear chemosignals than when neutral (Siniscalchi et al., 2016). Dogs also show a similar emotional response to others through smell (D'Aniello et al., 2018) and behave accordingly.

Furthermore, dogs and cats generate visual images when they hear vocalizations (Adachi et al., 2007; Takagi et al., 2019). Such interchanges of information across sensory modalities may be useful to animals because the available modalities may be unavailable at other times. Additionally, individuals are identified through several senses, such as appearance, voice, and smell. The contribution of auditory and olfactory communication to bond formation will need to be investigated in future studies.

CONCLUSION

Dogs and cats have both been integrated into human habits for improved access to food, and they use human signals to obtain information such as the location of food. However, they differ in their food acquisition situations. Dogs exhibit behaviors that require human cooperation while cats do not rely on humans, perhaps due to the nature of their ancestral species. Dogs first cooperated with humans as working animals, and cats were allowed in the human habitat to catch mice. However, today cats and dogs share an equal and similar ecological niche among humans.

It is particularly interesting that cats, originally solitary animals, can adapt to living in groups with humans and other cats. Most of the behaviors that cats exhibit toward humans were initially observed in mothers-kittens, suggesting that the behaviors seen in their adaptation to a group with humans were inherent. In the future, cats may acquire more dog-like abilities, such as more consistent and expressive gaze, through human selection. Investigating changes that cats may exhibit by selection would be helpful for understanding the evolutionary process of sociality in a broader context.

Dogs and cats use several senses to communicate with humans. Each of these senses contributes to the distinction between owner and stranger. Voices, smell, and other factors also foster the formation of bonds between dogs/cats and humans, and future research should investigate other perceptions that similarly may have been involved in the formation of bonds. The literature at present indicates that dogs and cats have their own adaptive communications that may have provided the basis for their mutually beneficial coexistence with humans.

AUTHOR CONTRIBUTIONS

HK, TK, ST, and MN wrote the manuscript. All authors contributed to the article and approved the submitted version.

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CORRECTION
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Corrigendum: The Gaze Communications Between Dogs/Cats and Humans: Recent Research Review and Future Directions

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In the original article, there was a mistake in **Table 1** as published. The references for the entry "Looked alternately at the food and the owner when it could access the food" (section "social reference") were incorrect. The corrected **Table 1** appears below.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

TABLE 1 | Gaze communication between dogs/cats and humans.

Dogs	References	Cats	References
Response to human gaze			
Stole food less often	Call et al., 2003; Kaminski et al., 2013	Avoided the gaze of familiar human	Koyasu and Nagasawa, 2019
Obeyed more commands of their owners	Schwab and Huber, 2006	Selected food from humans who looked at them	Ito et al., 2016
Fetched the toy that humans could see in the situation with two toys	Call et al., 2003		
Increased attention-getting behaviors	Ohkita et al., 2016		
Selected food from humans who looked at them	Gácsi et al., 2004		
Using human signals			
Used human pointing in the task of selecting one of two containers	Miklosi et al., 2005	Used human pointing in the task of selecting one of two containers	Miklosi et al., 2005
Used human gaze direction with pointing in the task of selecting one of two containers	Hare et al., 2002	Looked in the direction indicated by human gaze (with head movements)	Pongrácz et al., 2019
Looked in the direction directed by human gaze (with head movements)	Hare et al., 1998; Agnetta et al., 2000; Téglás et al., 2012; Met et al., 2014	Followed the container that humans visited in a situation with two food containers	Chijiiwa et al., 2020
Followed the container that humans visited in a situation with two food containers	Chijiiwa et al., 2020; Nagasawa et al., 2020		
Social reference			
Looked alternately at the food and the owner when it could access the food	Miklosi et al., 2005, Lazzaroni et al., 2020	Did not look alternately at the food and the owner when it could not access the food	Miklosi et al., 2005
Looked alternately at the strange object and the owner	Merola et al., 2012a,b	Looked alternately at the strange object and the owner	Merola et al., 2015
The role of gaze in bond formation			
Increased attention-getting behaviors in dogs, which function as attachment behaviors in response to human gaze	Ohkita et al., 2016	Eyeblink synchronization during mutual gazing	Koyasu et al., 2020
Dog owner's oxytocin secretion increased in response to the dog's gaze	Nagasawa et al., 2009		
An oxytocin-mediated positive loop of bond formation facilitated and modulated by gazing, like mother-infant	Nagasawa et al., 2015		
Eyeblink synchronization during mutual gazing	Koyasu et al., 2020		

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ORIGINAL RESEARCH
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Investigating Indirect and Direct Reputation Formation in Asian Elephants (*Elephas maximus*)

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Reputation is a key component in social interactions of group-living animals and appears to play a role in the establishment of cooperation. Animals can form a reputation of an individual by directly interacting with them or by observing them interact with a third party, i.e., eavesdropping. Elephants are an interesting taxon in which to investigate eavesdropping as they are highly cooperative, large-brained, long-lived terrestrial mammals with a complex social organisation. The aim of this study was to investigate whether captive Asian elephants (*Elephas maximus*) could form reputations of humans through indirect and/or direct experience in two different paradigms: (1) a cooperative string-pulling task and (2) a scenario requiring begging. Fourteen captive Asian elephants in Thailand participated in an experimental procedure that consisted of three parts: baseline, observation, and testing. In the observation phase, the subject saw a conspecific interact with two people—one cooperative/generous and one non-cooperative/selfish. The observer could then choose which person to approach in the test phase. The elephants were tested in a second session 2–5 days later. We found no support for the hypothesis that elephants can form reputations of humans through indirect or direct experience, but these results may be due to challenges with experimental design rather than a lack of capacity. We discuss how the results may be due to a potential lack of ecological validity in this study and the difficulty of assessing motivation and attentiveness in elephants. Furthermore, we highlight the importance of designing future experiments that account for the elephants' use of multimodal sensory information in their decision-making.

Keywords: eavesdropping, third-party evaluation, image scoring, social evaluation, third-party interactions, human-animal interactions, string-pulling, elephant cognition

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INTRODUCTION

Cooperation is defined as two or more individuals working together to obtain a mutual benefit and is frequently observed in group-living animals. For example, female elephants collectively take care of younger individuals in the herd (i.e., allomothering—Lee, 1987), wolves (*Canis lupus*) work together to hunt large prey (MacNulty et al., 2014), and male chimpanzees (*Pan troglodytes*) defend their territory together (Boesch and Boesch, 1989). The evolutionary mechanisms that underlie the expression of cooperation in social animals are well-understood (West et al., 2007), but how cooperation is maintained within a social group to increase an animal's chance of survival is not.

Reputation refers to knowing how an individual behaves in a typical situation based on what is known about that individual's behaviour in the past (Russell et al., 2008). It is another component in the social interactions of group-living animals and appears to play a key role in the establishment of cooperation. For example, when an individual has a reputation for "cooperation," they may have more opportunities to acquire desirable resources and partners than an individual known to be "non-cooperative," who may instead be excluded from interactions with others (Wu et al., 2016). Thus, reputation can also contribute to survival (Abdai and Miklósi, 2016).

Reputation can be formed through direct interactions between individuals or via observations of interactions by a third party, known as eavesdropping (Bonnie and Earley, 2007). Eavesdropping may be more cognitively demanding than forming reputations through direct interactions, as it requires individuals to remember and recognise behaviours from third-party interactions. However, eavesdropping is crucial to providing animals with the capacity to predict the behaviour of others while avoiding the costs of direct experiences (Subiaul et al., 2008). Despite the importance of eavesdropping, only a few studies on non-human animals have investigated this behaviour and even fewer have indicated that a particular animal has the capacity for eavesdropping.

For example, Bshary and Grutter (2006) investigated eavesdropping in client–cleaner fish (*Labroides dimidiatus*) interactions. In this experimental study, client fish observed a cleaner and a client model (a fake fish) on opposite sides of a tank. On one side of the tank, mashed prawn was smeared on the client model resulting in the cleaner foraging on it. This made the cleaner appear to behave "cooperatively." On the other side of the tank, another cleaner did not interact with a client model because prawn was not smeared on it; there was no client–cleaner interaction, so the client observer had no knowledge of the cleaner's cooperativeness. They found that the observing clients spent significantly more time next to the cooperative cleaner than the one with an unknown cooperation level, which suggests that the clients differentiated between the two cleaners and preferred the cooperative one. This was a clear demonstration of the fish's ability to eavesdrop. Although clients observed the cleaners interact with an inanimate client model, this study is impressive because it is the only controlled study to date that has investigated eavesdropping in animals performing natural behaviours, thus increasing the ecological validity of the results. Also, this was a conspecific-driven rather than experimenter-driven design. As it is difficult to control an animal's behaviour in an experiment, most studies on eavesdropping in animals involve interactions with humans. Thus, it would be logical to test species that are capable of acquiring information from humans, such as non-human apes (Bräuer et al., 2005) and dogs (*Canis lupus familiaris*) (Pongrácz et al., 2001).

Studies on eavesdropping typically involve animals observing human–human interactions in a begging situation, i.e., a generous person who gives food to a human beggar and a selfish person who refuses to give food. Russell et al. (2008) and Herrmann et al. (2013) tested chimpanzees, bonobos (*Pan paniscus*), and orangutans (*Pongo pygmaeus abelii*). Russell et al. (2008) tested gorillas (*Gorilla gorilla*) as well. These studies found that chimpanzees showed a significant preference for the generous person. A similar result was observed in orangutans in Herrmann et al. (2013) but not in Russell et al. (2008), and there was no significant preference by bonobos or gorillas. The positive results from the chimpanzees in these studies are contrasted by Subiaul et al. (2008, Experiment 1), where none of the seven chimpanzees showed a preference between the two humans. Subiaul et al. (2008, Experiment 3) conducted a follow-up experiment where chimpanzees observed humans interacting with a conspecific and found that three out of four chimpanzees chose the generous person on the first trial. However, these results should be considered with caution, as the sample size was small compared to Russell et al. (2008) and Herrmann et al. (2013), who tested 17 and 103 chimpanzees, respectively.

Enhancing the relevance of the interactions animals observe may be important in human–animal interaction studies on eavesdropping, as it could help them form a judgment of the humans. One potential confound to consider in such interspecific testing scenarios, however, is that these interactions are often highly artificial. In the wild, for instance, chimpanzee social interactions are exclusively between conspecifics, so chimpanzee–human eavesdropping studies, while informative, may lack ecological validity and should thus be interpreted with caution.

Eavesdropping on human–animal interactions might be more important for animals that live with humans, such as domesticated species, given that humans often provide them with valuable resources, such as food and shelter (Freidin et al., 2013). Thus, it would benefit them to form reputations of humans in order to choose the most appropriate person with whom to associate. Interestingly, results on domestic dogs and cats (*Felis silvestris catus*) have been mixed. In Rooney and Bradshaw (2006), dogs approached and preferred a person who won a tug-of-war game with a conspecific over the game's loser, suggesting that they were eavesdropping and formed a judgment that winners were desirable social partners. In contrast, Nitzschner et al. (2012) found that dogs showed no preference for a nice human, who interacted positively with a conspecific, or a human who ignored a conspecific. They only found a preference for the "nice" human compared to the "ignoring" human after the dogs had direct experience with them. Piotti et al. (2017) did not find evidence to support this, as dogs did not form a judgment of the experimenter based on her skilfulness or the quality of the interaction. Furthermore, a recent study on domestic cats indicated that they do not form reputations of humans based on direct experience, or on indirect interactions between humans and conspecifics (Leete et al., 2020). Thus, whether or not eavesdropping is a widespread phenomenon in non-human animals is still unknown (**Table 1** summarises the studies that have been published to date).

Apart from being the most studied species in eavesdropping research, chimpanzees and dogs are also among the most studied species in the field of comparative cognition in general.

TABLE 1 | Summary of experiments on reputation formation in animals.

Species	Interaction	Experience	Outcome	References
Chimpanzees, bonobos, orangutans, gorillas	Human–human	Indirect	Chimpanzees: nice > mean Other apes: no significant difference	Russell et al., 2008
				Herrmann et al., 2013
Chimpanzees, bonobos, orangutans	Human–human	Direct	Nice > mean	Experiment 1
		Indirect	Chimpanzees and orangutans: nice > mean Bonobos: no significant difference	Experiment 2
				Subiaul et al., 2008
Chimpanzees	Human–human	Indirect	No significant difference	Experiment 1
		Direct	Learned to discriminate between generous and selfish	Experiment 2
	Human–animal	Indirect	Generous > selfish	Experiment 3
Dogs	Human–animal	Indirect	Winner > loser of tug-of-war game	Rooney and Bradshaw, 2006
				Nitzschner et al., 2012
Dogs	Human–animal	Direct	Nice > ignoring	Experiment 1
		Indirect	No significant difference	Experiment 2
Dogs	Human–animal	Direct	No significant difference	Piotti et al., 2017
Cats	Human–animal	Indirect Direct	No significant difference	Leete et al., 2020

Chimpanzees are our closest living relatives and similar cognitive abilities in humans and apes would suggest common ancestry for complex cognition. Humans shaped the evolution of dogs through domestication (Hare and Tomasello, 2005), and looking at the social relationships between the species provides important clues about the effects of domestication on social abilities. However, in order to understand convergent evolution, it is important to study other evolutionarily distant animals that show similarities in cognition likely due to similarities in the environmental pressures they may have faced in their evolution. This field, known as convergent cognitive evolution, suggests behavioural flexibility, particularly in social problem-solving, may not be uniquely primate (Plotnik and Clayton, 2015). For example, elephants are an interesting taxon to test for eavesdropping because they are highly cooperative, large-brained, long-lived terrestrial mammals with a complex social organisation like chimpanzees (Byrne et al., 2009).

There is some evidence to suggest that elephants can form reputations of humans through direct experience. Bates et al. (2007) conducted a study in the Amboseli National Park, Kenya, where Maasai men demonstrate virility by spearing African elephants (*Loxodonta africana*), and Kamba agriculturalists pose little threat. They found that elephants showed greater fear when they detected the scent of garments previously worn by Maasai and reacted more aggressively to the red clothes that Maasai typically wear than to Kamba clothing. McComb et al. (2014) also found that elephants exhibited more defensive bunching and investigative smelling following playbacks of Maasai voices compared to Kamba voices. Furthermore, elephants exhibited these behavioural responses significantly more often when they heard the voices of Maasai men compared to Maasai women and Maasai boys. These results suggest that elephants had formed a bad reputation of Maasai men. Interestingly, Bates et al. (2007) found that elephants with no experience of spearing showed similar reactions as those that had interacted with Maasai men before. A possible explanation is that elephants had formed a bad reputation of Maasai men through indirect experience; however, this hypothesis would be very difficult to test experimentally with wild African elephants. Although there is little history of African elephants living in captivity in range countries, Asian elephants have a 4,000-year history of being tamed to live alongside humans in Asia. Thus, Asian elephants in Thailand—where more than 3,500 elephants live in captivity today—are ideal candidates for studying eavesdropping via human–animal interactions, as they are habituated to humans and interact with both familiar and unfamiliar people every day. They are also interesting to study from a comparative cognition perspective because they are not domesticated like dogs but have this long history of interacting with humans (Lair, 1997; Plotnik et al., 2013).

In the current study, we tested Asian elephants using an eavesdropping variation of the cooperative string-pulling task. Typically, in this test, two ends of a string must be pulled simultaneously to pull a platform baited with food rewards within reach. If only one end of the string, which is threaded around the platform, is pulled, the platform will not move and the string becomes unthreaded, making the baited platform inaccessible (Hirata and Fuwa, 2007). It is a well-established paradigm that has been used to test cooperation in many species, including Asian elephants (Plotnik et al., 2011), and has been used to study direct reputation formation in chimpanzees. After the chimpanzee subjects had experience using the apparatus with two conspecific partners that differed in their collaborative skills, they learned to recruit the more effective partner, which suggests that they had some understanding of the partner's role in the task (Melis et al., 2006). Although this task is often used to test cooperation between conspecifics, it has also been used to test cooperation between humans and dogs (Ostojić and Clayton, 2014) and wolves (Range et al., 2019a,b). Furthermore, in Experiment 2 of Range et al. (2019b), dogs and wolves were successful in recruiting a human partner to solve the cooperative string-pulling task.

Based on the elephants' experience with humans and their social complexity, as well as their success on the cooperative string-pulling task (Plotnik et al., 2011), we used, for the first time, the string-pulling task to investigate Asian elephants' ability to form reputations about cooperative and non-cooperative humans. The aim of the current study was to test whether Asian elephants can form reputations of humans through indirect and/or direct experience. In Experiment 1, we investigated whether elephants could differentiate between a cooperative and a non-cooperative partner in a string-pulling task. In Experiment 2, we simplified the design and investigated whether elephants could differentiate between a generous and a selfish partner in a begging situation, without the need for cooperation. We hypothesised that elephants derive and act on information about unfamiliar humans through reputation-like inferences after observing them interact with a conspecific and/or after directly interacting with them. Therefore, we predicted that elephants would significantly prefer the cooperative/generous partner over the non-cooperative/selfish partner. Direct reputation formation is a prerequisite for eavesdropping; thus, we predicted that elephants would at least show a significant preference for the cooperative/generous partner after direct experience.

EXPERIMENT 1: STRING-PULLING TASK

Methods

Ethical Statement

This study was approved by the National Research Council of Thailand (Protocol #0002/848 and #0402/838). Ethical approval was obtained from the "Ethik und Tierschutzkommission" of the University of Veterinary Medicine Vienna (Protocol #ETK-15/12/2018) and Hunter College's Institutional Animal Care and Use Committee (Protocol #JP-Elephant Eavesdropping 1/22). The individual humans who participated in this study have either given written informed consent to publish photographs and videos containing their images in the **Supplementary Materials**, or we de-identified images by blurring faces when we were unable to get written informed consent.

Subjects

Twelve female captive Asian elephants (*Elephas maximus*) from the Golden Triangle Asian Elephant Foundation (GTAEF) living on the properties of the Anantara Golden Triangle Elephant Camp and Resort and the Four Seasons Tented Camp in Chiang Rai, Thailand, participated in the experiment between March and May 2019 (see **Table 2**). However, four elephants were excluded. One did not pass training (Lanna), one successfully obtained the food without the need for cooperation (Boonruam), and two were influenced by their mahouts (caretakers) in such a way that the elephants' choices may have been affected (Bo and Kumtoon). Each mahout is mostly responsible for a single elephant for extended periods of time, although during this study, mahouts did sometimes change due to circumstances beyond our control.

Apparatus

The string-pulling apparatus was a 3 m (W) × 92 cm (L) tray with wheels attached to the bottom of the tray. The tray was placed on top of a 1.4 m (W) × 3 m (L) × 60 cm (H) metal frame with six adjustable legs. A single piece of a 16.5-m-long, 7-mm-thick rope was threaded through PVC pipe frames around the back and sides underneath the tray so that the loose ends appeared out of two openings on either side of the front of the apparatus, leaving 1.6 m of rope available in the testing area to pull upon approach. The apparatus was such that if only one end of the rope was pulled, the tray could not move, but rather the rope slid out of the frame and the non-pulled end of the rope became unavailable. Adjacent to each end of the rope, 2.2 m apart from each other, there were two clear buckets that extended 55 cm out of the tray. Hence, to successfully obtain the food, both ends of the rope needed to be pulled simultaneously to move the tray forward so that the buckets could pass under the volleyball net.

Experimental Setup

The experiment was conducted in a large field (10.6 m × 92 m) at the Anantara Golden Triangle Elephant Camp and Resort in Chiang Rai, Thailand. The two apparatuses were placed 2 m apart from each other and on one side of a 10-m volleyball net that was strung between two posts, forming a transparent but reliable barrier between the elephants and the apparatus (Plotnik et al., 2011). The elephants learned quickly that they were not allowed to pass beyond the barrier and thus stopped at the rope ends upon approach. The observer's area was partitioned by a red rope 5.2 m away from the volleyball net to create space so that the subject (hereafter also referred to as the observer) could not interfere with the interactions between the human partner and the demonstrator elephant during the observation phase.

The whole experiment was recorded by three cameras. One Panasonic HD consumer video camera was placed on a tripod in between the two apparatuses facing the observer in a position that captured the whole observer's area. One GoPro Hero 4 Black was positioned by the volleyball net to gain a side view of the testing area, and another GoPro Hero 4 Black was placed on a tripod on a post that separated the observer's area and the apparatuses to gain a view of the whole testing area (see **Figure 1**).

Procedure

The experiment consisted of training sessions and two test sessions.

Training

It was important that each elephant was able to use the string-pulling apparatus reliably and understood that she could choose which apparatus to use in the test phase. Thus, the main experimenter trained all the subjects and the demonstrator elephant, which took between 2 and 11 sessions ($M = 4.7$, $SD = 2.5$). Each subject was required to successfully cooperate with a human who stood in front of one of the two baited apparatuses in 5 out of 6 trials before she could participate in the study.

TABLE 2 | List of subjects' participation.

Elephant	Sex	Age (years)	Experiment 1	Experiment 2
Bo*	F	41	Excluded (demonstrator)—mahout influence	Yes (demonstrator)
Boonruam	F	59	Excluded—obtained food without cooperation	No
Boonsri	F	51	Yes	Yes
Dah	F	17	Yes	Yes
Jathong	F	28	Yes	Yes
Kumtoon	F	15	Excluded—mahout influence	Yes
Lanna	F	31	Excluded—did not pass training	Yes
Mae Moo	F	55	No	Yes
Mae Noi	F	21	Yes	Yes
Bleum	F	21	Yes	Yes
Prae	F	29	Yes	No
Pumpui	F	42	Yes	No
Yui	F	27	Yes	No (demonstrator)
Riang Ngun	M	42	No (demonstrator)	Yes

**Participated as an observer first and then acted as a demonstrator for half of the subjects after she had completed testing.*

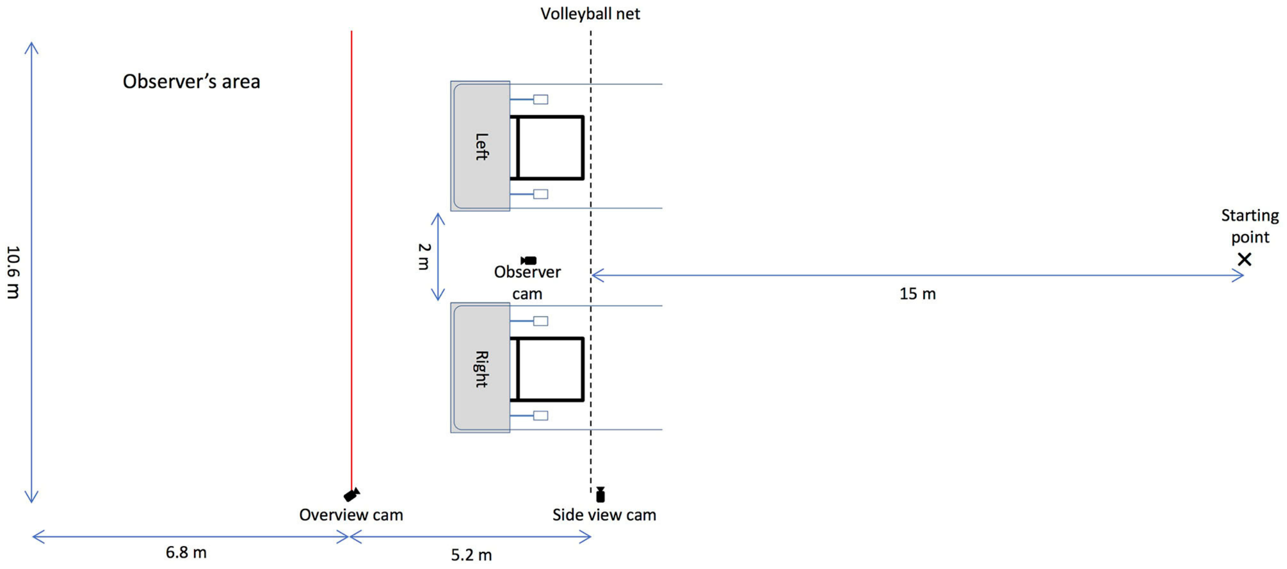

FIGURE 1 | Schematic depiction of the setup of the string-pulling experiment. The two string-pulling apparatuses were placed 2 m apart from each other on one side of a volleyball net. In the baseline and the test phase, the subject stood at the starting point and each human partner stood in front and at the centre of one of the apparatuses. In the observation phase, the subject stood in the observer's area on the left (separated by a red rope) and the demonstrator stood at the starting point.

Session 1

Throughout the experiment, two unfamiliar Thai human females acted as the partners—one wore white clothes and the other wore black. Asian elephants rely heavily on non-visual sensory information, such as auditory cues (Jacobson and Plotnik, in press), so each partner also said a predetermined sentence when they interacted with the demonstrator elephant to help the observer distinguish between the two partners visually and auditorily. Their role and colour of clothes were randomised and fixed within-subjects and counterbalanced between-subjects.

The male elephant (Riang Ngun) acted as the demonstrator for half of the subjects, and a female elephant (Bo) was selected to act as the demonstrator for the other half of the subjects. Each elephant was accompanied by a mahout for safety, who stood by the elephant and did not interact with him/her.

Prior to testing, the elephants could explore the environment freely for ~5 min to familiarise themselves with the location. The experiment consisted of three parts.

Baseline This phase was only conducted in Session 1 and tested whether the observer preferred one person prior to observing any third-party interactions with the demonstrator. Neither string-pulling apparatus was baited, and the ropes were placed on the tray behind the volleyball net so it was inaccessible to the elephant. Each human partner stood 5 m in front and at the centre of one of the apparatuses (the partners' positions were

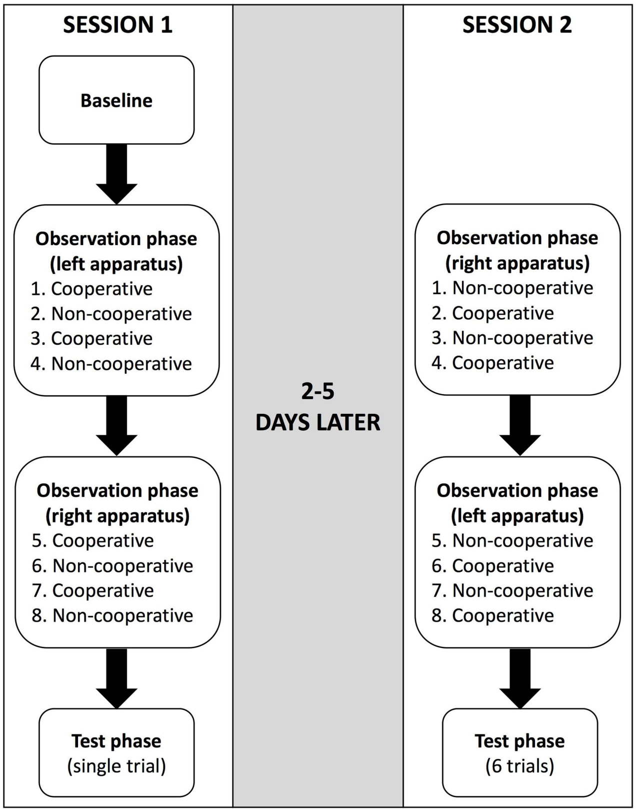

FIGURE 2 | Flowchart illustrating an example of the procedure in the string-pulling experiment. The order of the string-pulling apparatus that was used first (left or right) and the partner who interacted with the demonstrator first (cooperative or non-cooperative) were randomised and counterbalanced between subjects.

randomised). Each partner held a piece of food (apple or banana based on the elephant's preference) in their hands.

The elephant was positioned at a starting point marked by spray paint on the ground in the testing area (15 m away and equidistant from the partners). The mahout stood behind the elephant and released her to walk forward. When the elephant approached within arm's length of one of the partners, the first gave the food to the animal, followed immediately by the other calling the elephant to offer food. If the elephant did not approach either partner (e.g., she foraged or stood still), the mahout brought the elephant back to the starting point and released her again until a choice was made.

After this trial, the partners left the testing area, the observer was moved to the observer's area, and the demonstrator elephant was moved to the starting point in the testing area.

Observation phase First, the main experimenter only baited one of the string-pulling apparatuses (randomised and counterbalanced across subjects) and laid the two ends of the rope into the testing area. A partner stood in front and at the centre of it. The main experimenter then indicated to the mahout that the phase could begin. The mahout released the demonstrator from the starting point so he/she could walk forward and pull a rope. The demonstrator could choose which rope to pull, and then the partner moved to the opposite side of the apparatus. The observer then witnessed one of the following scenarios depending on the partner with whom the demonstrator interacted:

A. Cooperative: when the demonstrator picked up the rope, the partner picked up the other end of the rope and said in Thai, "Let's eat!" in a friendly tone. They pulled the ropes simultaneously so that the tray moved forward and they both ate the food.
B. Non-cooperative: when the demonstrator picked up the rope, the partner did not touch the apparatus and said in Thai, "I won't help!" in an unfriendly tone and walked away from the apparatus. Thus, the tray did not move forward and they were unsuccessful in obtaining the food.

After the interaction, the partner left the testing area, the main experimenter reset and re-baited the apparatus and the procedure was repeated with the second partner. After the demonstrator had interacted with each partner twice, the main experimenter placed the ropes on the tray behind the volleyball net, set up and baited the other apparatus, and then repeated the procedure. Overall, the demonstrator interacted with each partner twice alternately on one apparatus and twice alternately on the other apparatus (i.e., four interactions with each partner occurred in total—see **Figure 2**).

After the observation phase, the demonstrator left the testing area and the observer was moved to the testing area. The main experimenter set up and baited both apparatuses for the test.

Test phase Each partner stood directly in front and at the centre of one of the apparatuses (the partners' positions were randomised). As the observer stood at the starting point, the mahout stood behind and released the elephant to walk forward. When the elephant arrived at the apparatuses, she could choose a rope to pull and thus which partner with whom to cooperate. If the elephant did not approach a partner within 1 min, the mahout brought the elephant back to the starting point and the main experimenter added a handful of sunflower seeds into the buckets of each apparatus to increase her motivation. When the apparatuses were baited, the mahout released the elephant again until a choice was made or the mahout stopped the experiment if he felt the elephant did not want to participate anymore. This only occurred for one elephant (Pumpui) who did not complete the last trial (see **Table 3**).

We defined a choice response by the rope the elephant touched. Once a choice had been made, the partner acted the same way as she did in the observation phase, i.e., the cooperative partner pulled the other rope and the non-cooperative partner moved away and did not touch the apparatus. After this trial, Session 1 was over and the partners and the observer left the testing area.

Session 2

The subject was tested 2–5 days later; she experienced the observation phase, where the order of the partners and the first apparatus used was counterbalanced, and six trials in the test phase. The partners' positions were semi-randomised such that they never stayed in the same position more than twice in a row.

Coding and Statistical Analyses

The observer must pay attention to the partner's actions to understand their different roles. Thus, we coded the subject's attention during the observation phase from the footage from the observer camera, which was synchronised with the footage from the overview and side view cameras and merged into one video.

We defined the beginning of the interaction as the moment the demonstrator touched the rope, and the end of the interaction as the time when the mahout asked the demonstrator to retreat and the partner left the testing area. During the cooperative interactions, we coded whether the subject was attentive at the moment when the demonstrator pulled the rope with the cooperative partner and/or while the demonstrator ate the food. During the non-cooperative interactions, we coded whether the subject was attentive at any time while the demonstrator pulled the rope.

We coded whether the subject was attentive or not in each interaction during the observation phase in both sessions. We defined the subject as being attentive towards the third-party interaction if the subject's head was oriented towards the interaction and her ears were out or her trunk was pointed towards the direction of the interaction. We defined the subject as not being attentive if her head and/or body were not oriented towards the interaction or she was attentive to the other partner. Furthermore, if the mahout interfered in any way that caused the subject to turn away from the interaction, point her trunk towards the mahout, or respond to a mahout direction, we coded her as not attentive.

All statistical analyses were carried out using R (version 3.6.2; R Core Team, 2019). HLJ and RD coded 20% of the videos for interobserver reliability, which was analysed using the intraclass correlation coefficient from the R package "irr" (version 0.84.1, Gamer et al., 2012) (ICC (two-way, agreement) = 0.717, $F = 5.97$, $p < 0.001$). HLJ and RD then each coded half of the videos.

We conducted generalised linear mixed-effects models (GLMMs) with binomial error structure and logit link function (McCullagh and Nelder, 1989), which were fitted using the function glmer of the R package "lme4" (version 1.1–21, Bates et al., 2015). Sixty-four observations were made with eight individuals.

We included attentiveness in the model by determining the proportion of interactions the elephants were attentive in the observation phase of both sessions. Then, we split the data into two subsets: the first subset, called "string-pulling eavesdropping" (comprising the baseline, the single trial in Session 1 and the first trial in Session 2), tested whether elephants formed a reputation of the humans based on their indirect experience; given the limited experience after Session 1, we argue that the first trial of Session 2 is still based on observation rather than the brief direct experience a few days prior. The second subset, called "string-pulling reputation-learning" (comprising the latter five trials), tested whether elephants formed a reputation of the humans based on their direct experience.

For the string-pulling eavesdropping subset, the full model included trial as a test predictor (factor with three levels), attentiveness (covariate) as a control predictor with fixed effects, and subject ID as a random intercept. The response variable was the subject's choice to approach the cooperative partner. Since we counterbalanced and hence controlled for the partners' roles, positions, and colour of clothes, we did not add those or demonstrator ID as control predictors in any of the analyses to reduce the complexity of the model.

For the string-pulling reputation-learning subset, the full model included z-transformed trial as a test predictor (covariate), attentiveness as a control predictor with fixed effects, subject ID as a random intercept and z-transformed trial as a random slope (Schielzeth and Forstmeier, 2009; Barr et al., 2013) within subject ID. To ease convergence, we changed the optimizer used by the function glmer to "bobyqa" (Jacobson, n.d.). We excluded the correlation between the random intercept and slope because it was estimated to be essentially 1, which is indicative of it not being identifiable (Matuschek et al., 2017).

We compared the full model to the null model which lacked trial (z-transformed in the string-pulling reputation-learning subset) in the fixed-effects part for both subsets. We determined the confidence of model estimates by means of a parametric bootstrap (function bootMeer of the package lme4). We assessed model stability by comparing the estimates obtained from the models based on all data with those obtained from models with the individuals excluded one at a time, which revealed the string-pulling eavesdropping subset to be very unstable (see the range of estimates in **Supplementary Table 1**) and the string-pulling reputation-learning subset to be unstable in some parts (see the range of estimates in **Supplementary Table 2**).

Results

String-Pulling Eavesdropping

Five out of eight elephants chose the cooperative partner in the single trial of Session 1, and three out of eight elephants chose the cooperative partner in the first trial of Session 2. Only one elephant (Boonsri) chose the cooperative partner in the first two trials across the two sessions (i.e., the single trial of Session 1 and the first of six trials in Session 2—see **Table 3**).

The likelihood ratio test comparing the full and null model revealed that trial had a marginally non-significant effect ($\chi^2 = 5.943$, $df = 2$, $p = 0.051$), and attentiveness did not have a significant effect ($\chi^2 = 2.884$, $df = 1$, $p = 0.089$) on the elephants' choice to approach the cooperative partner. There was no significant difference in the elephants' choice for the cooperative partner between the single trial of baseline and the Session 1 single trial ($p = 0.239$, see **Supplementary Table 1**). Elephants were significantly less likely to choose the cooperative partner in the first trial of Session 2 compared to the baseline ($p = 0.042$, see **Supplementary Table 1**). We then re-levelled the factor trial such that the reference level was the single trial in Session 1 and found that there was no significant difference in the

TABLE 3 | Results of the string-pulling experiment.

Elephant	Eavesdropping subset			Reputation-learning subset
	Baseline Did she choose the cooperative partner?	**Session 1 (one trial)** Did she choose the cooperative partner?	**Session 2** Did she choose the cooperative partner in the first trial?	**Session 2** No. of times she chose the cooperative partner
Boonsri	Yes	Yes	Yes	2/6
Mae Noi	Yes	Yes	No	2/6
Yui	Yes	Yes	No	2/6
Dah	Yes	Yes	No	1/6
Pumpui	Yes	Yes	No	3/5
Prae	No	No	Yes	6/6
Bleum	Yes	No	Yes	3/6
Jathong	Yes	No	No	2/6

elephants' choice to approach the cooperative partner between the single trial of Session 1 and the first trial of Session 2 ($p = 0.218$, see **Supplementary Table 1**).

String-Pulling Reputation-Learning

The likelihood ratio test comparing the full and null model revealed non-significance for trial ($\chi^2 = 0.892$, $df = 1$, $p = 0.345$) and attentiveness ($\chi^2 = 0.469$, $df = 1$, $p = 0.494$) on the elephants' choice to approach the cooperative partner (see **Supplementary Table 2**). Thus, trial and attentiveness did not have a significant effect on the animals' choice to approach the cooperative partner in the latter five trials.

Discussion

In Experiment 1, we compared the elephants' choice of the cooperative partner in the one baseline trial, the single trial of Session 1, and the first trial in Session 2 to analyse whether the elephants eavesdropped. They did not significantly choose the cooperative partner after observing the two humans interact with a conspecific (Session 1 single trial) compared to when they had no prior experience with them (baseline). However, we did find that elephants significantly chose the non-cooperative partner over the cooperative one in the first trial of Session 2 compared to when they had no prior experience with the partners (baseline). This result is surprising because the elephants chose the non-cooperative partner and so were unsuccessful in obtaining the food reward, which contrasts with our prediction. A closer look at our data reveals that the significant effect was due to 7 out of 8 elephants choosing the cooperative partner in the baseline and only 3 out of 8 choosing the cooperative partner in the first trial of Session 2. Therefore, the elephants did not choose the two partners equally at random in the baseline, which created a false-positive effect. Furthermore, five elephants chose the cooperative partner in the single Session 1 trial and three chose the cooperative partner in the first trial of Session 2, which are both close to chance level (four out of eight elephants). A high level of performance would be needed across all elephants (e.g., at least seven out of eight) for the result to be convincing for such a small sample size, thus we cannot make strong conclusions about eavesdropping in elephants from this result.

We compared the elephants' choice for the cooperative partner in the latter five trials in Session 2 to analyse whether the elephants demonstrated direct reputation formation. Overall, they did not significantly choose the cooperative partner more often than the non-cooperative partner and they did not learn to choose the cooperative partner after successive testing. Therefore, the results do not provide support for our hypothesis that elephants can form reputations of humans based on indirect or direct experience and attentiveness did not appear to be a factor. While the first trial of Session 2, like the only trial of Session 1, is based on observation, the additional five trials of Session 2 are based on direct experience. It is thus noteworthy that one elephant (Prae) chose the cooperative partner in every trial in Session 2. However, because she did not choose the cooperative partner in the single trial of Session 1 and no other elephants performed as consistently as she did in Session 2, it is not possible to determine whether she formed a reputation of the cooperative partner early in Session 2 or learned to choose that partner due to direct experience over the course of six successive trials.

Russell et al. (2008) found that the top eight most attentive chimpanzees (54–80% attention, mean scores per subject over all trials) demonstrated eavesdropping, but the bottom eight (13–50% attention) did not. The behavioural coding reveals that the elephants in the present study demonstrated similarly high attentiveness (69–88%, mean scores per subject over all trials), except one elephant (Jathong), who scored 38% (see **Figure 3**). Prae was the most attentive, thus she may have demonstrated reputation formation. However, overall attentiveness did not have a significant effect on the elephants' choice for the cooperative partner, possibly due to our small sample size. An alternative explanation is that elephants may require different types of information to eavesdrop than chimpanzees. This could be because chimpanzees are more visual, while Asian elephants may be more reliant on acoustic and olfactory information in their environments (e.g., Plotnik et al., 2013, 2019; Ketchaisri et al., 2019); thus, they may need more non-visual sensory information to understand the partner's different roles.

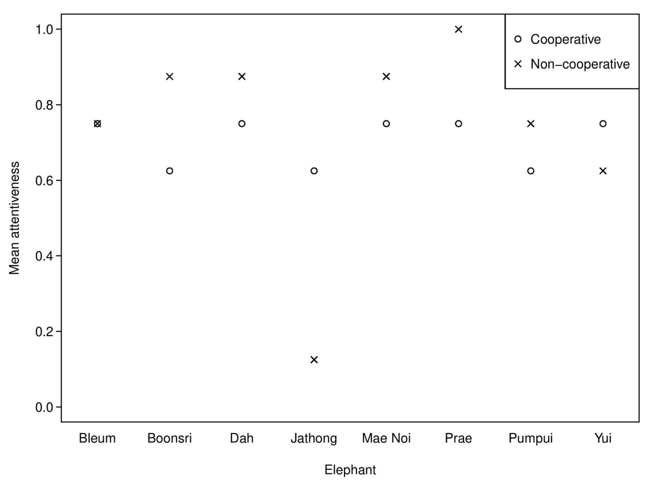

FIGURE 3 | Mean attentiveness in the observation phase across Session 1 and 2 of the string-pulling experiment.

Our findings are not in line with Melis et al. (2006), who found that chimpanzees recruited the effective partner through direct experience, and Range et al. (2019b), who found that dogs and wolves were successful in recruiting a human partner in the cooperative string-pulling task. A possible reason for the discrepancy between the results is that chimpanzees (Boesch and Boesch, 1989) and wolves (MacNulty et al., 2014) hunt cooperatively, whereas elephants forage individually. Moreover, it has been hypothesised that the cooperative skills of dogs with humans were inherited from their wolf ancestors (Canine Cooperation Hypothesis—Range and Virányi, 2015). As dogs were domesticated, they have a lot of experience with humans and heavily rely on them for food (Freidin et al., 2013), whereas captive Asian elephants are not domesticated and although they can cooperate with humans, they often work closely with a single individual, their mahout (Lair, 1997). Therefore, using the cooperative string-pulling task to investigate human–elephant interactions may lack ecological validity.

We used a variation of the cooperative string-pulling task to test eavesdropping because this paradigm has been used to test cooperation in elephants (Plotnik et al., 2011) and it seemed plausible that they would be flexible enough to generalise it to another context. In Plotnik et al. (2011)'s study, the elephants waited for their conspecific partner and did not pull the rope if their partners did not either. However, it is possible that, in the current study, the use of two different human partners may have made the task overly complex. The elephants may not have understood that one partner acted cooperatively and the other non-cooperatively.

Another potential explanation for these negative results is that the experimental apparatus itself may also have been too complicated. The two loose rope ends appeared out of openings on either side of the string-pulling apparatus, and the two apparatuses were placed side by side. Therefore, four rope ends were laid out at a similar distance to each other in the test phase. As the elephant was positioned in the centre between the two apparatuses at the start of each trial, it may have been difficult for the elephant to understand that the two central ropes were attached to different apparatuses when they approached, even though they had experience with the experimental setup in the test phase during training. We considered having the partners stand by the two central ropes so the elephant could only choose the outer ropes of each apparatus; however, this was not possible due to safety concerns.

For the reasons explained above, we conducted a follow-up experiment with a simpler design to test whether elephants can form reputation judgments of two humans—one generous and one selfish—after observing them interact with a conspecific and/or after directly interacting with them in a begging situation, like Subiaul et al. (2008, Experiment 3). This setup may also be more ecologically valid, as the elephants are often fed by unfamiliar people, such as tourists.

We also included two additional conditions in the follow-up experiment. As eavesdropping is defined as acquiring information through observing third-party interactions, we added an asocial control condition, where the partners acted "generously" and "selfishly" to an invisible third party. We predicted that, after observing third-party interactions, elephants would prefer the generous partner over the selfish partner in the experimental condition, but there would be no preference for either partner in the asocial control condition. Furthermore, the elephants did not have equal experience with the partners in Experiment 1, as their experience depended on who they approached in the test phase. Therefore, we added a "direct experience" condition to standardise their direct experience with each partner in the follow-up experiment. As direct reputation formation is a prerequisite for eavesdropping, we predicted that elephants would at least show a preference for the generous partner after direct experience.

EXPERIMENT 2: BEGGING SITUATION

Methods

Subjects

Ten captive Asian elephants, nine females and one male, from GTAEF participated in the experiment between August and September 2019 (see **Table 2**).

Materials and Experimental Setup

The experiment was conducted at the same location as Experiment 1; however, the string-pulling apparatuses were removed and a 5.7-m volleyball net was strung in the centre and perpendicular to the 10-m volleyball net. Three dots were marked on the ground on either side of the testing area; the bucket of food was placed on the central dot, which was marked 2.5 m away from the volleyball net. The human partners stood on each of two dots, one on either side of the centre dot/bucket and 1.1 m away from it. Additionally, some improvements were made to the testing area; two holding pens were built on opposite sides of the testing area to aid the elephants' starting point, two 10-m volleyball nets were strung one on top of the other on the left side of the field to prevent the elephants from foraging on bamboo adjacent to it, and a rope was tied to posts on the right side of the field to keep the elephants in the testing area.

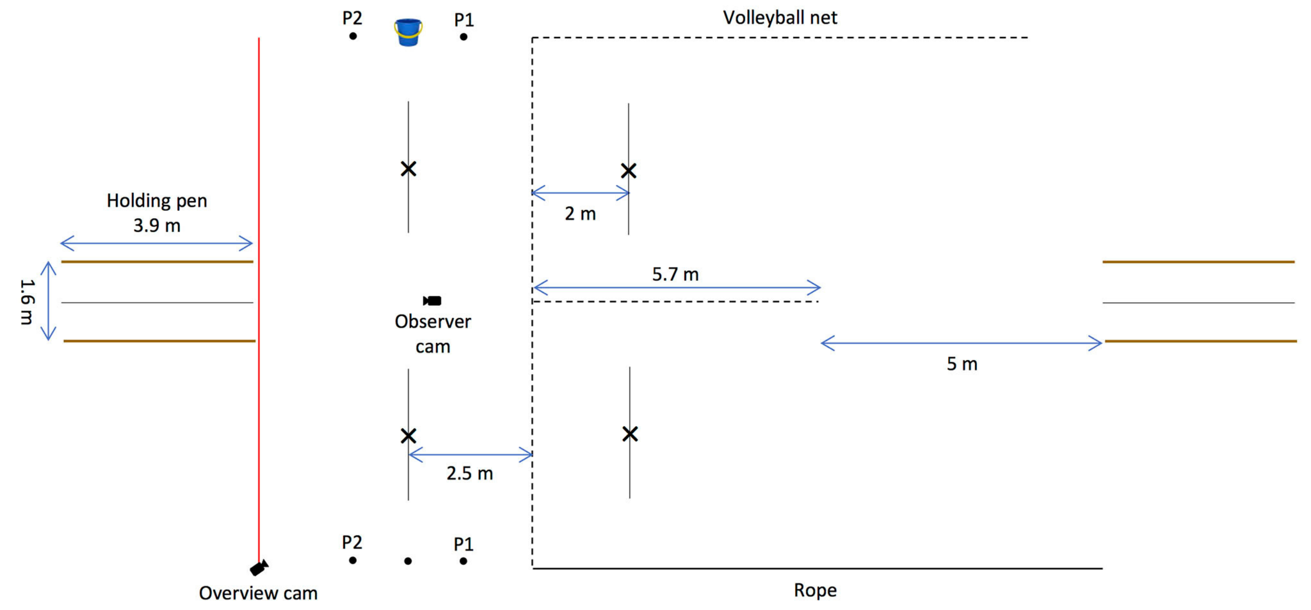

FIGURE 4 | Schematic depiction of the setup of the begging experiment. A 5.7-m volleyball net was strung in the centre and perpendicular to the 10-m volleyball net. Three dots were marked on the ground on either side of the testing area; the bucket of food was placed on the central dot, and the human partners stood on either side of the bucket (P1 and P2). The crosses marked 2 m away on the right side of the volleyball net indicate where the human partners stood in the baseline and the test phase in the experimental and control conditions. The lines marked 2.5 m away on the left of the volleyball net indicate when the elephant made a choice response in the experimental and control conditions. In the direct experience condition, the experimental setup was mirrored. Two holding pens were built on opposite sides of the field to aid the elephants' starting point.

The whole experiment was recorded by one GoPro Hero 4 Black that was placed on a tripod 2 m behind the volleyball net facing the observer and another one that was placed on a tripod on a post to gain a view of the whole testing area (see **Figure 4**).

Experimental Design

There were three conditions (see **Figure 5**):

1. Experimental: the subject observed the partners interact with the demonstrator.
2. Control: the demonstrator was absent—the subject observed the partners perform the same actions without an elephant. The control was conducted so that if eavesdropping was observed in the experimental condition, we would be able to discern whether the elephants' responses were due to the partner observing the social interaction between partner and demonstrator, or whether the partners' actions *per se* (moving forward or away with a bucket of food) were sufficient to allow a discrimination between them.
3. Direct experience: there was no demonstrator or observer—the subject directly interacted with the partners. In this condition, the experimental setup was mirrored, i.e., the subject was in the holding pen in the testing area and the partners were on the other side of the volleyball net in the baseline and test phase.

This was a repeated-measures design; half of the sample experienced the experimental condition first, and the other half experienced the control condition first. All subjects experienced the direct experience condition after they were tested in the experimental and control conditions. There was a 4–12-day break between each condition.

Procedure

The procedure resembled that of Experiment 1 with some minor differences. The experiment consisted of two test sessions.

Session 1

Apart from the main experimenter and a research assistant, there were two human partners who were unfamiliar to the elephants in each condition. The pair of partners remained stable within conditions; there were a total of six human partners in the experiment, who were all Thai females. In the first condition, one partner wore white clothes and the other wore black. In the second condition, one partner wore a white spot-patterned poncho and the other wore a dark camouflage print poncho. In the direct experience condition that was conducted last, the partners wore white and black clothes again. As in Experiment 1, the partners said different, predetermined sentences when they interacted with the demonstrator to help the observer distinguish the two partners visually and auditorily. Their role and colour of clothes were randomised and fixed within-subjects and counterbalanced between conditions between-subjects.

A female elephant (Yui) acted as the demonstrator for half of the subjects, and another female (Bo) was selected to act as the demonstrator for the other half of the subjects after she had completed testing. In this experiment, mangoes were used to

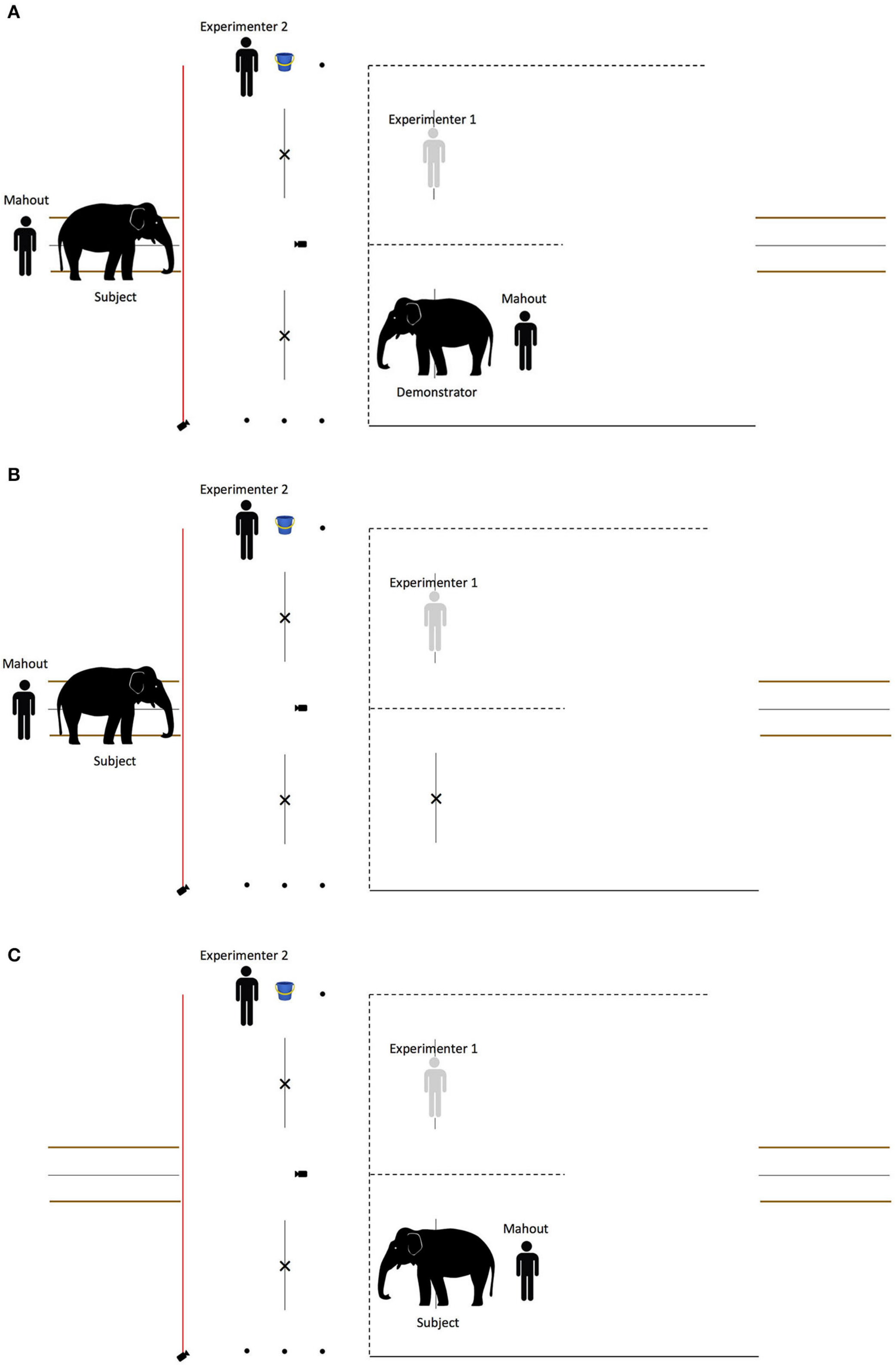

FIGURE 5 | Schematic depiction of the observation phase in the begging experiment. In the experimental condition **(A)**, the subject observed the partners interact with the demonstrator. In the control condition **(B)**, the demonstrator was absent—the subject observed the partners perform the same actions without an elephant. In the direct experience condition **(C)**, there was no demonstrator or observer—the subject directly interacted with the partners.

increase the elephants' motivation to participate, as it is a more high-value food reward than apples and bananas.

Prior to testing, the elephants could explore the environment freely for ∼5 min to familiarise themselves with the location. The experiment consisted of three parts.

Baseline This phase was only conducted in Session 1. In the experimental and control conditions, the subject was placed in the holding pen in the observer's area. The partners stood in front of the volleyball net, 5 m away from each other; each person held a mango in their hands, and their positions were randomised.

The elephant's starting point was in the holding pen, 5.2 m away from the volleyball net; when the elephant was centred, the research assistant untied the red rope and the mahout stood behind the elephant and released him/her to walk forward. A choice response was made when the elephant approached a partner and was fed. The partner who was not chosen called the elephant forward to feed him/her. If the elephant did not approach either partner, the mahout brought the elephant back to the starting point and released him/her again until he/she made a choice.

After this trial, both partners left the testing area and the observer camera was set in place. The mahout moved the subject back to the holding pen, the rope was tied again, and the demonstrator was positioned on one side of the testing area (randomised and counterbalanced across subjects and conditions).

In the direct experience condition, the baseline was identical to the experimental and control conditions, but the experimental setup was mirrored. When the elephant approached a partner and was fed by her, the partner who was not chosen walked towards the elephant to feed him/her, as there was a volleyball net between them. After this trial, the subject was positioned on one side of the testing area (randomised and counterbalanced across subjects).

Observation phase In the experimental condition, the main experimenter placed a bucket of mangoes on one side of the testing area (randomised and counterbalanced across subjects) and the partners stood on either side of it (P1 and P2 in **Figure 4**), each holding a clear bucket. The demonstrator stood on the opposite side of the partition to the partners. The first partner (standing in P1) took a mango from the bucket, entered the testing area, and faced the demonstrator. The observer witnessed one of the following scenarios depending on which partner the demonstrator interacted with:

A. Generous: the partner dropped the mango into the bucket and said in Thai, "Here you go!" in a friendly tone. Then she walked forward and put the bucket under the volleyball net so that the demonstrator could reach the food and eat it.
B. Selfish: the partner dropped the mango into the bucket and said in Thai, "You can't have it!" in an unfriendly tone. Then she turned around and walked away from the elephant.

After the interaction, the partner walked to P2 and the second partner stood in P1. We controlled the partners' positions because P2 was closer to the subject in the observer's area. Hence, we ensured the time the partners spent close to the subject was equal to avoid the possible confound that elephants may simply choose the partner that spent more time close to them in the observation phase. The procedure was repeated with the second partner, and after the demonstrator had interacted with each partner twice, the partners and the demonstrator swapped sides and the main experimenter moved the bucket of food to the opposite side of the testing area. Overall, the demonstrator interacted with each partner twice alternately on each side of the volleyball net, thus there were four interactions with each partner in total. After the observation phase, the demonstrator left the testing area and the main experimenter removed the bucket of food and the observer camera. In the control condition, the observation phase was the same as the experimental condition; however, the demonstrator was not present, i.e., the partners "interacted" with an invisible demonstrator. In the direct experience condition, the observation phase was the same as the experimental condition; however, the demonstrator was not present and the observer was in the demonstrator's position, i.e., the partners interacted with the subject.

Test phase In the experimental and control conditions, the partners stood 2 m behind the volleyball net, each holding a clear bucket with a mango inside, and their positions were randomised. The mahout centred the elephant, then the research assistant untied the red rope and the mahout stood behind the elephant and released him/her to walk forward. If the elephant did not approach a partner within a minute, the mahout brought him/her back to the starting point and released him/her again until he/she made a choice or the mahout stopped the experiment if he felt the elephant did not want to participate anymore. This only occurred for one elephant (Mae Noi) who completed two trials in the experimental condition (see **Table 4**).

We defined a choice response as when the elephant crossed the line marked 2.5 m in front of the volleyball net. Once a choice had been made, the human partner acted the same way as she did in the observation phase, i.e., the generous partner walked forward to feed the elephant and the selfish partner turned around and walked away.

In the direct experience condition, the test phase was identical to the experimental and control conditions; however, the experimental setup was mirrored and a choice response was made when the elephant moved to one side of the volleyball net strung in the centre of the testing area. After this trial, Session 1 was over and the partners and the subject left the testing area.

Session 2

The subject was tested 2–5 days later; he/she experienced the observation phase, where the order of the partners was counterbalanced and the demonstrator and partners stood on the opposite side of the testing area from Session 1. There were six trials in the test phase, in which the partners' positions were semi-randomised so that they never stayed in the same position more than twice in a row.

Coding and Statistical Analyses

As in Experiment 1, we coded the subjects' attention from the footage from the observer camera, which was synchronised with the footage from the overview camera and merged into one video. We used the same ethogram to code whether the subject was attentive towards the interaction.

We defined the beginning of the interaction as when the partner stood facing the demonstrator before she dropped the food into the bucket, and the end of the interaction as when the partner moved to leave the testing area or after the demonstrator had eaten the food, whichever came last. During the interactions with the generous partner, we coded whether the subject was attentive during the moment of food exchange or when the demonstrator ate the food. During the interactions with the selfish partner, we coded whether the subject was attentive when she turned around to walk away from the demonstrator.

HLJ and RD coded 20% of the videos for interobserver reliability, which was analysed using the intraclass correlation coefficient from the R package "irr" (version 0.84.1) (ICC (two-way, agreement) $= 0.873$, $F = 14.7$, $p < 0.001$). HLJ and RD then each coded half of the videos.

Statistical analyses were also conducted in the same way as Experiment 1. We conducted GLMMs with binomial error structure and logit link function, which were fitted using the function glmer of the R package "lme4" (version 1.1–21). Two hundred and thirty-six observations were made with 10 individuals.

We split the data into two subsets. The first compared the experimental and control condition. In the experimental condition, the single trial in Session 1 and the first trial in Session 2 tested for eavesdropping. The justification for this interpretation is the same as in Experiment 1. In the control condition, the single Session 1 trial and the first trial in Session 2 tested whether the elephants' responses were due to the partner observing the social interaction between partner and demonstrator, or whether the partners' actions *per se* (moving forward or away with a bucket of food) were sufficient to allow a discrimination between them.

We included attentiveness in the model by determining the proportion of interactions the elephants were attentive in the observation phase of both sessions, and then we split the data into two further subsets: "begging eavesdropping" (comprising the baseline, the single trial in Session 1 and the first trial of Session 2 in the experimental and control condition) to test whether elephants formed a reputation of the humans based on their indirect experience, and "begging reputation-learning" (comprising the latter five trials in the experimental and control condition) to test whether elephants formed a reputation of the humans based on their direct experience.

The second subset analysed the direct experience condition separately, which we refer to as the "direct experience" subset. In this subset, we also split the data into two further subsets: Session 1 (comprising the baseline and single trial) tested whether elephants formed a reputation of the humans based on four brief interactions and Session 2 (comprising all six trials) tested whether elephants need more interactions, across two separate days, to form a reputation of the humans.

For the begging eavesdropping subset, the test predictors were trial (factor with three levels) and condition (factor with two levels). The control predictors were condition order (factor with two levels) and attentiveness (covariate). Therefore, the full model included an interaction between trial × condition × condition order, attentiveness as a fixed effect, and subject ID as a random intercept.

The full model for the begging reputation-learning subset included an interaction between z-transformed trial × condition × condition order and all lower order terms this encompasses, attentiveness as a fixed effect, subject ID as a random intercept, and z-transformed trial as a random slope within subject ID.

To ease convergence, we fitted both models using the optimizer "bobyqa." Then, we compared the full model to the null model for both sessions, from which we removed trial (z-transformed in the begging reputation-learning subset), condition, and the interactions in which they were involved.

For Session 1 in the direct experience subset, the full model included trial as a test predictor (factor with two levels) and subject ID as a random intercept. To ease convergence, we used the optimizer "bobyqa." Then, we compared the full model to the null model, where trial was removed from the fixed effects part of the model.

For Session 2 in the direct experience subset, the full model included z-transformed trial as a test predictor (covariate), subject ID as a random intercept, and a z-transformed trial as a random slope within subject ID. To ease convergence, we used the optimizer "bobyqa." Then, we compared the full model to the null model, where z-transformed trial was removed from the fixed effects part of the model.

We assessed model stability by comparing the estimates obtained from the models based on all data with those obtained from models with the individuals excluded one at a time. This revealed that the model for the begging eavesdropping subset was very unstable (see the range of estimates in **Supplementary Table 3**). The model for the begging reputation-learning subset was also, in some parts, very unstable (see the range of estimates in **Supplementary Table 4**). The model for Session 1 of the direct experience subset had good stability. However, the model had extremely large estimates (see **Supplementary Table 5**) and a large standard deviation estimated for the random effect of individual (*SD* $= 36.517$), likely due to lack of data; thus, the model is not trustworthy. For Session 2 of the direct experience subset, the model was moderately stable (see the range of estimates in **Supplementary Table 6**).

Results

As previously outlined, each condition (experimental and control) consisted of two sessions. The first two trials across the two sessions (i.e., the single trial of Session 1 and the first of six trials in Session 2) of the experimental condition compared to those of the control condition test for eavesdropping. The latter five trials in Session 2 test for direct reputation formation.

TABLE 4 | Results of the begging experiment (experimental and control condition).

Elephant	Condition							
	Experimental				Control			
	Baseline Did he/she choose the generous partner?	Session 1 (one trial) Did he/she choose the generous partner?	Session 2 Did he/she choose the generous partner in the first trial?	Session 2 No. of times he/she chose the generous partner	Baseline Did he/she choose the generous partner?	Session 1 (one trial) Did he/she choose the generous partner?	Session 2 Did he/she choose the generous partner in the first trial?	Session 2 No. of times he/she chose the generous partner
Dah	Yes	Yes	Yes	6/6	Yes	No	Yes	5/6
Bo	No	Yes	Yes	4/6	No	Yes	No	3/6
Bleum	Yes	Yes	Yes	2/6	Yes	Yes	Yes	6/6
Lanna	Yes	Yes	Yes	2/6	Yes	No	Yes	1/6
Kumtoon	No	No	Yes	5/6	Yes	No	No	1/6
Boonsri	No	No	No	3/6	Yes	Yes	Yes	3/6
Jathong	No	No	Yes	3/6	No	No	No	1/6
Mae Moo	No	No	No	3/6	No	Yes	No	1/6
Riang Ngun	Yes	No	No	2/6	No	No	No	3/6
Mae Noi	No	No	No	0/2	Yes	No	No	1/6

The presentation order of experimental and control conditions was counterbalanced.

Begging Eavesdropping

In the single trial of both the experimental and control conditions in Session 1, four out of 10 elephants chose the generous partner. In Session 2, six elephants chose the generous partner in the first trial of the experimental condition and four elephants chose the generous partner in the first trial of the control condition. Four elephants chose the generous partner in the first two trials in the experimental condition, and two elephants chose the generous partner in the first two trials in the control condition. Only one elephant (Bleum) chose the generous partner in both trials and in both conditions. Additionally, Bleum chose the generous partner in every trial in both sessions of the control condition and another elephant (Dah) chose the generous partner in every trial in both sessions of the experimental condition (see **Table 4**).

The likelihood ratio test comparing the full and null model did not reveal significance for attentiveness ($\chi^2 = 0.056$, $df = 1$, $p = 0.812$) or the interaction between trial × condition × condition order ($\chi^2 = 0.726$, $df = 2$, $p = 0.696$). Thus, none of the predictors had a significant effect on the animals' choice to approach the generous partner (see **Supplementary Table 3**).

Begging Reputation-Learning

The likelihood ratio test comparing the full and null model also did not reveal significance for attentiveness ($\chi^2 = 0.194$, $df = 1$, $p = 0.660$) or the interaction between trial number × condition × condition order ($\chi^2 = 1.992$, $df = 1$, $p = 0.158$). Thus, none of the predictors had a significant effect on the animals' choice to approach the generous partner (see **Supplementary Table 4**).

Direct Experience

Six out of 10 elephants chose the generous partner in the Session 1 single trial, and only one elephant (Lanna) consistently chose the generous partner in all six trials in Session 2 (see **Table 5**).

For Session 1, the likelihood ratio test comparing the full and null model revealed significance ($\chi^2 = 8.881$, $df = 1$, $p = 0.003$), indicating that elephants were significantly more likely to choose the generous partner in the Session 1 single trial compared to the baseline ($p = 0.008$, see **Supplementary Table 5**). However, as stated in the methods, the model was very unstable, likely due to lack of data, and thus the model is not trustworthy. Therefore, we are unable to interpret this result.

For Session 2, the likelihood ratio test comparing the full and null model did not reveal significance ($\chi^2 = 0.098$, $df = 4$, $p = 0.755$). Therefore, trial had no significant effect on the animals' choice to approach the generous partner.

As the results were non-significant for both experiments, we tested whether the elephants had a side bias. We conducted a Heterogeneity G-test (McDonald, 2014) for 10 out of 14 elephants that completed more than one condition (the four elephants who only participated in the string-pulling experiment were excluded from the analysis). We found that there was no side bias across conditions for either the left or the right side ($Gh = 3.969$, $df = 9$, $p = 0.913$, $Gt = 4.00$, $df = 10$, $p = 0.947$).

TABLE 5 | Results of the begging experiment (direct experience condition only).

Elephant	Baseline Did they choose the generous partner?	Session 1 (one trial) Did they choose the generous partner?	Session 2 No. of times they chose the generous partner
Dah	Yes	Yes	2/6
Bo	No	Yes	2/6
Bleum	No	Yes	4/6
Lanna	No	No	6/6
Kumtoon	No	Yes	2/6
Boonsri	No	Yes	3/6
Jathong	No	No	2/6
Mae Moo	Yes	Yes	1/6
Riang Ngun	No	No	4/6
Mae Noi	No	No	4/6

Discussion

In Experiment 2, we found that the elephants did not differentiate between the generous or selfish partner in a begging situation after indirect or direct experience. Although we found that elephants significantly preferred the generous partner after four brief interactions with the two partners (the single trial in Session 1) compared to when they had no prior experience with them (baseline), a closer look at our data reveals that the significant effect was due to eight out of 10 elephants choosing the selfish partner in the baseline and six out of 10 choosing the generous partner in the single trial in Session 1. Therefore, as in Experiment 1, the elephants did not choose the two partners equally at random in the baseline, which again created a false-positive effect. The number of elephants that chose the generous partner in Session 1 (six out of 10 elephants) was also close to chance level (i.e., five out of 10 elephants). A high level of performance would be needed across all elephants (at least eight out of 10) for the result to be convincing for such a small sample size; thus, we cannot make strong conclusions about eavesdropping in elephants from this result. Furthermore, the elephants did not differentiate between the generous or selfish partner after direct experience across two separate days. Therefore, the results do not support the hypothesis that elephants can form reputations of humans.

We ruled out lack of attentiveness as a possible explanation for why we did not find evidence of eavesdropping, as attentiveness had no significant effect on the animals' choice to approach the generous partner. However, the elephants appeared to be somewhat less attentive in this experiment (37–72% attention, mean scores per subject over all trials) (see **Figure 6**) compared to Experiment 1 (38–88%) (see **Table 6**). Out of the five elephants that participated in both experiments, four elephants' attentiveness scores decreased. A possible explanation is the fatigue effect; as half of the subjects had already been tested in a similar setup in Experiment 1, it is possible that they learned that food was rewarded at 50/50 chance in the test phase. If they learned this, and such rewards were sufficient motivation to participate, there may have been little additional motivation to pay attention to the observation phase in this experiment.

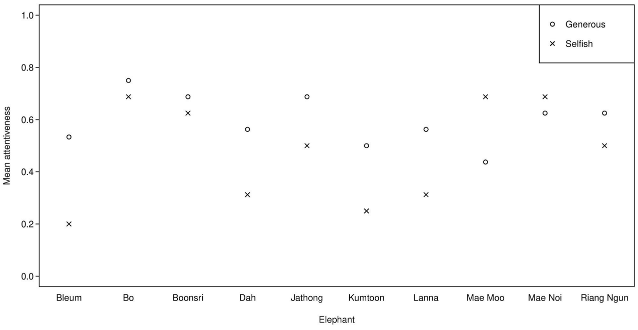

FIGURE 6 | Mean attentiveness in the observation phase across Session 1 and 2 for the experimental and control condition of the begging experiment.

The Experiment 2 attentiveness scores of the three elephants that did not participate in Experiment 1 were lower than the Experiment 1 attentiveness scores of four of the five elephants whose data were included from both experiments (see **Table 6**). Thus, these results cannot be explained by the fatigue effect. This may be because the string-pulling apparatus used in Experiment 1 made a loud noise when the tray moved forward, which may have caught the elephants' attention. In this experiment, the main auditory cue to distinguish between the partners was their voices when they spoke to the demonstrator, but the action of walking towards or away from the demonstrator was the crucial information the subjects needed to attend to in order to distinguish the partners' roles. The partners did not speak before the test trials—if they had, it may have helped the elephants to differentiate between the partners and approach the generous partner based on the location of the speaker. Therefore, the elephants may not have been able to distinguish the partners' roles in this experiment based on the primarily visual information and the limited auditory information.

TABLE 6 | Mean attentiveness scores per subject over all trials in the observation phase in Session 1 and Session 2 in both experiments (DP = did not participate at all in this experiment; E = data were excluded from analysis due to mahout interference).

	Experiment 1: String-pulling task		**Experiment 2: Begging situation**	
Elephant	**Attentiveness**	**Interactions scored (out of 16)**	**Attentiveness**	**Interactions scored (out of 32)**
Prae	88%	16	DP	NA
Dah	81%	16	44%	32
Mae Noi	81%	16	66%	32
Boonsri	75%	16	66%	32
Bleum	75%	16	37%	30
Jathong	38%	16	59%	32
Pumpui	69%	16	DP	NA
Yui	69%	16	DP	NA
Bo	E	NA	72%	32
Mae Moo	DP	NA	56%	32
Riang Ngun	DP	NA	56%	32
Lanna	DP	NA	44%	32
Kumtoon	E	NA	37%	32

GENERAL DISCUSSION

The results indicate that Asian elephants did not differentiate between a cooperative and a non-cooperative partner in a cooperative string-pulling task, nor did they differentiate between a generous and a selfish partner in a begging situation. We ruled out lack of attentiveness and side bias as possible explanations for the results in both experiments; thus, our results do not support the hypothesis that elephants can form reputations of humans. However, given the small sample size in our study and the poor model stability for the analysis of the experiments, we reach this conclusion with caution. Furthermore, as we discuss below, based on our knowledge of elephants in captivity, particularly in Southeast Asia, as well as previous research on African elephants in the wild, we believe further research that takes the elephants' multimodal sensory perception into account (Jacobson and Plotnik, in press) may yield different results.

Our results are not in line with Subiaul et al. (2008), which found some evidence for reputation formation through direct (Experiment 2) and indirect (Experiment 3) experience in chimpanzees. In Experiment 2 of Subiaul et al. (2008), five out of seven chimpanzees learnt to discriminate between the generous and selfish partners after 15–75 direct experiences, and one of those failed to maintain a preference for the generous partner. In our study, the elephants only had eight direct experiences with each partner over two sessions; thus, we may have found evidence for direct reputation formation if the elephants had had more direct experience. In Experiment 3 of Subiaul et al. (2008), three chimpanzees chose the generous partner on the first trial and one developed a preference after successive testing. Taken together, it is difficult to conclude that the chimpanzees demonstrated reputation formation based on these results, as the sample size was very small.

Direct reputation formation is a prerequisite for eavesdropping, and as the elephants did not demonstrate reputation formation even after direct experience, it is unsurprising that we did not find evidence of eavesdropping. However, it is unusual that we did not find evidence of direct reputation formation. A possible explanation is that elephants cannot form reputations of humans, but this is highly unlikely. Previous research has shown that African savanna elephants are able to distinguish between humans after direct experience based on visual, olfactory, and auditory cues (Bates et al., 2007; McComb et al., 2014). The relationship between individual humans and Asian elephants in captivity throughout Southeast Asia also makes it highly unlikely that they cannot form reputations of people. Elephants in logging or tourist camps often work closely with a specific human mahout over many years and not only recognise and respond to that individual mahout but also have been known to respond differentially to other mahouts, veterinarians, or managers (Lair, 1997).

There are also several differences between the earlier studies (Bates et al., 2007; McComb et al., 2014) and the present study that may explain the discrepancy in the results. First, it is important to acknowledge that Asian and African savanna elephants are different species with different ecologies. Recent research comparing elephants' ability to follow human-provided social cues has found differences between African (Smet and Byrne, 2013) and Asian elephants (Plotnik et al., 2013; Ketchaisri et al., 2019); therefore, it is possible that there are significant species-level differences between African and Asian elephant behaviour and ecology (Ketchaisri et al., 2019). Second, the previous research focused on wild African elephants, where interactions with Maasai men may be costly; thus, it was crucial for the elephants' survival to eavesdrop in that context. If the elephants chose the non-cooperative or selfish person in the present study, there was a small cost of not receiving a small food reward. Therefore, it is likely that elephants can form reputations of humans, but our experimental designs lacked ecological validity and thus the elephants did not respond as they would in a context with which they were familiar (either in the wild or captivity). It would be interesting to test reputation formation using human–elephant interactions in a more ecologically valid non-foraging context, for example, farmers who react differently to wild Asian elephants raiding their croplands, or a similar experiment to the present one with humans interacting with captive Asian elephants in a helping situation.

Another explanation for the negative results is that the elephants in the present study may not have been motivated to choose the cooperative or generous partner for a small food reward. Humans provide much of the food for captive Asian elephants, but the elephants also spend some time during the day foraging for themselves. Domesticated species such as dogs rely heavily on humans for food and food rewards (Freidin et al., 2013); thus, a food-sharing situation may be more relevant for dogs. Nevertheless, we tried to test the elephants at their maximum motivation by conducting the experiments early in the morning before they were fed by their mahouts or tourists and while the temperature was not too hot. We also tried to increase their motivation by feeding them high-value foods, such as mangoes, bananas, apples, and sunflower seeds. We could not restrict their diet the night before to increase their motivation, which can be done with other species such as dogs. Elephants eat roughly 250 kg of food a day; thus, restricting their diet for any length of time is neither practical nor ethical.

A limitation of the present study is that we could not be certain whether the elephants were paying attention to the third-party interactions in the observation phase. Although we operationalised attentiveness, it is difficult to define attentiveness in elephants. Therefore, although the interobserver reliability for our behavioural coding was based on specific behavioural measures, we could not be certain that the elephants were paying attention to the observations. While the elephants may have been paying attention during trials, they may have been watching the conspecific or the food rather than the human partner's actions/identity, which is necessary for them to understand the partners' different roles. Previous research on dogs showed that they did not develop a preference for the generous person even after many direct experiences because they were too focused on the food (Nitzschner et al., 2012). Thus, if the elephants were not watching the partners' actions, this would explain why they did not differentiate between the partners.

Another limitation is that our experiments were mainly visual tasks and elephants rely on more non-visual sensory information, such as auditory and olfactory cues (Plotnik et al., 2013, 2014, 2019; Schmitt et al., 2018, 2020; McArthur et al., 2019; Jacobson and Plotnik, in press). The elephants did have access to complementary visual, acoustic, and olfactory cues in our study; apart from the individuals' smell, the partners wore contrasting clothes and said different sentences when they interacted with the demonstrator. Furthermore, there was an audible noise when the apparatus moved in the string-pulling experiment and whenever food was placed into the buckets in both experiments. However, these cues may not have been salient enough for the elephants to distinguish between the two partners. The majority of studies on eavesdropping in animals to date have used visual tasks, as it is easiest to distinguish the partners' roles by having them perform different actions, and it makes sense to use this kind of experimental setup to test visual animals such as dogs, cats, and primates. However, we may learn more about eavesdropping in elephants if future research is designed using primarily auditory information, such as a playback experiment.

We used GLMMs to analyse whether the elephants' choice for the cooperative/generous partner differed before and after the observation phase, and our results suggest some issues with this analysis and our study design. We conducted a choice test because this seemed to be the best way to measure eavesdropping in elephants. Some previous studies have used proximity to an individual to measure eavesdropping in animals (e.g., Bshary and Grutter, 2006; Russell et al., 2008; Nitzschner et al., 2012; Leete et al., 2020). This is a particularly good measure for dogs as they tend to seek human contact, but it is not a good measure for elephants because they would be unlikely to approach a human unless food was involved. Consequently, a choice test can only be used once or twice to measure eavesdropping, as any more experience with the partners may lead to direct reputation formation. We were only able to test 8–10 elephants, so there were only 16 data points in the first experiment (string-pulling task) and 40 data points in the second experiment (begging situation with two conditions). We found that elephants did change their choice after the observation phase, but these were found to be false positives because the elephants did not choose equally at random in the baseline, and ultimately, the critical analyses came down to examination of the raw data. Thus, conducting a GLMM may be problematic if there are not enough data to measure the response accurately. In situations where a larger sample size is not possible, it might be worth considering alternative means of evaluating and presenting data, such as a single-case multiple-baseline AB design. With this design, the outcome variable is measured on a few "cases" (e.g., subjects) in a baseline phase (the A phase) and in an experimental phase (the B phase) (Bulté and Onghena, 2009; Bouwmeester and Jongerling, 2020; Levin et al., 2020). Then, the effect of the experimental phase is analysed using visual inspection of the pattern of observations in each phase and randomisation tests. As each case serves as its own control, this design may allow researchers to be more confident that the observed effect is attributed to the change in phase rather than extraneous variables and thus might be a good choice for future studies.

We had to remove several control variables from the GLMMs to reduce complexity, e.g., experimenter ID, role of experimenter, the colour of the experimenter's clothes, and experimenter position. Although we randomised and counterbalanced these variables, it would have been better to include them in the model or change the study design so that these variables did not need to be controlled for in the model, e.g., if each subject was tested with different pairs of individuals as experimenters. Finally, all previous studies on eavesdropping did not include a baseline to test whether there was a preference for an experimenter (e.g., Russell et al., 2008; Subiaul et al., 2008; Nitzschner et al., 2012; Herrmann et al., 2013; Piotti et al., 2017). Therefore, they assumed that the animals did not prefer an experimenter before the observation phase and their initial choice would be at chance level, i.e., 50%. However, our study shows that this is an important consideration—had we not conducted the baseline and included it in the analysis, we may have interpreted the results very differently. Therefore, we suggest that future experiments should have a larger sample size if possible, control for confounding variables, and include a baseline.

In conclusion, we tested whether Asian elephants can form reputations of humans in two different paradigms: (1) a cooperative string-pulling task and (2) a begging situation. Although we did not find evidence to support our hypothesis that elephants can form reputations of humans after indirect or direct experience, our study aids in our understanding of human–elephant interactions and informs our development of future species-specific research paradigms that focus on ecological validity within the socio-cognitive domain. Our research highlights the importance of considering sensory perception in socio-cognitive tasks, particularly those involving interspecific interactions. Further research on eavesdropping and reputation formation is needed because it could help explain how knowledge about humans spreads socially in elephants. In addition, a greater understanding of the role of elephant cognition in the elephant's interactions with humans could have important implications for improving captive elephant management, particularly as it relates to the management of mahout–elephant relationships. Finally, the flexibility of the elephant's decision-making process, particularly as it pertains to their decisions regarding whether to interact with specific humans, could be relevant for mitigating the increasing conflict between wild elephants and humans due to habitat loss in elephant range countries.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

This study was reviewed and approved by the National Research Council of Thailand (Protocol #0002/848 and #0402/838). Ethical approval was obtained from the Ethik und Tierschutzkommission of the University of Veterinary Medicine Vienna (Protocol #ETK-15/12/2018) and Hunter College's Institutional Animal Care and Use Committee (Protocol #JP-Elephant Eavesdropping 1/22).

AUTHOR CONTRIBUTIONS

HLJ, FR, SMP, RD, and JMP designed the study and refined the methodology. HLJ conducted the experiments. HLJ and RD coded the videos. HLJ analysed the data and drafted the manuscript. FR, SMP, RD, and JMP contributed to the analyses and to the writing of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.604372/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Providing an Outdoor Exercise Area Affects Tie-Stall Cow Reactivity and Human-Cow Relations

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Confinement and restriction of movement are a reality for most dairy cows. Providing outdoor access is one method to increase movement opportunities. However, leading cows to an outdoor exercise area increases their exposure to manipulations different from those of an indoor housing system. These situations have the potential to induce fear reactions, which can lead to injuries for the cow and danger or economic losses for the farmer. Our aim was to evaluate the development of the human-cow relationship and general reactivity of cows after a 12-week period of outdoor access provision in winter, summer and fall. A total of 16 cows in the winter, 16 in the summer, and 15 in the fall were enrolled in the study and either allocated to the treatment (Out) or stayed in the tiestall (NonOut). A human reactivity test and suddenness test were performed before and after the 12-week treatment period. In winter and to a lesser extent in fall, Out cows had a better human reaction score compared to NonOut cows, suggesting that cows with outdoor access during the winter associated human approaches with positive events. Conversely, no difference in the human reaction score was found between treatments during the summer. For summer and fall, Out cows did, however, show a decrease in their reaction score to the suddenness test compared to NonOut cows. The results of the human reactivity test in the summer suggested that cows with outdoor access did not associate the manipulation with a positive event. Interestingly, this result is not due to the cows being more frightened, since the suddenness test suggested that the Out cows were less fearful than NonOut cows. The way in which cows were led to the outdoor area could explain the differences in cow responses. Here, summer cows faced greater movement restrictions during trips to the outdoor area than in the winter, which may have been negatively perceived by the cows. We conclude that, besides the provision of outdoor access, the manner in which cows are handled during these events may have significant impacts on their reactions and could facilitate future handling.

Keywords: dairy cows, behavioral robustness, well-being, emotions, handling

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INTRODUCTION

Farm animals are often selected for their high production capacities. On occasion, behavioral characteristics can generate deficits or problems of adaptation (1, 2). The intensification of dairy production has led to changes in the management and housing parameters for animals, which now require new adaptations from them. Farm animals, particularly in intensive milking systems, can be subjected to many manipulations, which they are not accustomed to or could be considered as aversive, such as for certain medical interventions. These manipulations can cause significant stress in the animal (3). In times of stress, the animal's reaction can be variable, unpredictable, and dangerous both for them and their handlers (4–7). A balanced emotional reaction will allow the animal to respond to a potentially dangerous stimulus without becoming overwhelmed. This will prevent animals from over-reacting to novel situations, particularly during handling, and thus reduce injury risk for themselves and their handler.

Handling is an important risk in animal farming. Although cows are relatively docile animals, they can be dangerous and aggressive when situations displease or frighten them (6). Previous situations that involve discomfort have been associated with difficult handling. For example, moving cows for hoof-trimming results in more fearful and aggressive behaviors compared to directing them to daily milking (7). Numerous studies have shown that an animal's early experiences during handling strongly affect their future responses (8, 9) and more generally, the human-animal relationship (10). Other studies have shown a direct link between human behavior and cow behavior (11), where aversive manipulations can impair the relationship with humans [for review: (12)]. For example, Breuer et al. (13) found that heifers that were negatively handled had a greater flight distance toward humans and were more stressed than positively handled cows.

The provision of exercise is recommended to improve animal well-being and foot health (14, 15), and increase behavioral opportunities [review by (16)]. For tie-stall cows, this implies introducing many stimuli and additional human manipulations that they are not used to. Cows may be afraid and react unpredictably to these situations, or even aggressively, which may impact animal and human welfare. Providing stimulation can also help the animal to respond in a more appropriate way and therefore adapt better to situations (17, 18).

The objective of this research was to study the impact of regular exercise provision in an outdoor area, in winter, fall and summer seasons, on the reactivity and relationship of tie-stall cows with humans. Two behavioral tests were carried out: a human relationship test and a suddenness test for reactivity. Our hypothesis predicted that the daily manipulation of animals, combined with an positive outing experience, would improve the human-animal relationship. In addition, the enrichment provided by access to an outdoor exercise area may help the animal become less reactive to sudden events by building more adapted behaviors.

MATERIALS AND METHODS

Animal and Housing Conditions

Forty tie-stall housed Holstein dairy cows were selected from the resident herd at the McGill University Macdonald Campus Dairy Complex (QC, Canada). During the study, cows were housed in a tie-stall barn consisting of cubicle tie stalls (stall width of 1.3 m, bed length of 1.9 m, stall length of 2.1 m) with rubbermats, a 2 cm depth of wood shavings for bedding, and concrete alleyways. Cows within a pair were positioned to alternate in adjacent stalls. They had access to water *ad libitum*, and feed rations (average of 21.1 kg/d of TMR comprised 48.0% hay, 46.7% silage, 4.3% protein supplement, and 1.0% vitamin and mineral supplement) were distributed 4 times per day to ensure that feed was always available. Cleaning of the alleyways and stalls occurred 4 times per day, in equal intervals before and after outings. Fresh bedding was provided as needed to maintain a 2 cm depth of wood shavings per stall. The outdoor exercise area was a pen delimited by electric wires within a grassland (300 m²). In winter, there were snow cover and wood chips and in summer/fall, the grass was cut. The surface per cow averaged 25 m^2 across seasons. The size of pens varied between and within seasons and each group of cows was allocated to a new pen each week. In winter and fall, cows were allocated to pens of different sizes across the trial (min-max: 10-40 m² per animal); in the fall, the size of the paddock was always the same (39 m² per animal). An alleyway going from the barn to each pen allowed the handler to move the animals to their respective pens.

Procedures

General Process

Enrolled cows (excluding companion cows) were randomly allocated to 3 seasons, for a total of 16 in the winter, 16 in the summer, and 15 in the fall. This study was part of a series of trials examining the effects of exercise access in tie-stall cows and the number of animals enrolled was chosen according to several objectives (most notably: cow locomotor activity). Within each season, the cows were randomly assigned to one of two groups (Out or NoOut), and balanced and paired by parity and stage of lactation (Parity: 2.2 ± 1.22; DIM: 140.7 ± 71.12). Treatment cows (Out) were taken outdoors to an exercise area, while control cows (NonOut) were kept in the tie-stall. Outings took place 5 days a week each morning during 12 weeks. If some cows were in heat, they were not led outside to avoid injuries related to their excitement. Out cows were taken outdoor along with one not tested companion (Winter, Summer) or with the two other cows (Fall). This was done to ensure that all cows could have at least one conspecific with which to engage in social interactions. With all "Out" groups outside in the exercise yard, there was a total of 16 (Winter, Summer) or 15 (Fall) cows in the exercise yard at once (including trial and companion cows). All groups were put in separate paddocks. Out cows with their companion cow(s) were taken outdoors, pair by pair (or in trio), by being untied and equipped with a halter and moved to their outdoor exercise area for 2 to 3 h each morning. When released from the tie-stall, cows were halter-led by a handler through the barn until the outdoor. Then, the

TABLE 1 | Numbers of tested cows by treatment, phase and seasons.

	Winter		Summer		Fall	
Phase	**Before**	**After**	**Before**	**After**	**Before**	**After**
N NonOut	8	7	8	8	9	9
N Out	6	8	8	7	6	6

handler let go of the halter and moved the cows through an outdoor walking corridor, and finally directed them toward an outdoor exercise enclosure. Handling was more restrictive in summer than in fall, and in fall than in winter trials, partly due to changes in the flooring conditions of the alleys leading to the outdoor yard: cows moved forward differently according the floor stability and the weather. Handling was carried out according to a pre-established and standardized protocol to ensure the most consistent handling possible between cows, and was adapted for each season (**Supplementary Material S1**).

Two behavioral tests were performed: a human test and a suddenness test. These tests were carried out on all cows before and after the 12 weeks treatment period (**Table 1**). Not all cows could be tested at all times, due to estrus on testing days (baseline), or due to a lack of treatment application or a combination of events including estrus, weather, and health conditions (after treatment application period).

Cows were randomly subjected to the two behavioral tests on three consecutive days with not more than one test per day. The same test was not carried out on two neighboring cows in a single day, and the tests were equally distributed across groups each day. The suddenness test, which can be disruptive to other cows in proximity to the test cow, was always done after the human test.

Behavioral Tests

Human Test

The test is adapted from the procedure by Herskin et al. (19) and similar to Schmied et al. (20). The test involved two individuals: a test person who is used as stimulus, and an observer. The test person was an unfamiliar female dressed in blue work coat, different from the one that takes out the animals. She was the same for the winter and summer seasons, but was different in fall for technical reasons. However, the stature and clothes were noticeably similar. To begin, the observer ensured that all cows were standing. If they were lying down, she clicked her tongue then gave a little push on the rump if necessary; this method being usually and very regularly used by farm members throughout the day. The observer then positioned herself at the end of the row, at least 2 stalls away from the target cow, and performed live scoring. After waiting 5 min, in order to avoid any influence of the forced standing up, the test person stood in front of the target cow at a distance of 1.30 m from the tierail and captured the test cow's attention but to avoid a stretched chain at the start of the test (see **Video S1** in Supplementary material). When she was ready, the observer started the timer and then, the test person approached the test cow every 5 s according to the following sequence:

- Stage 1: 1 step, arms placed alongside the body
- Stage 2: 1 step, arms placed alongside the body
- Stage 3: One arm stretched out at ∼45°
- Stage 4: Outstretched hand placed on the chain at the base of the neck

The observer noted the reaction of the cow at each stage according to the following numerical scores:

- Score−3: Steps back (steps >2), chain stretched to the maximum,
- Score−2: Steps backs (1 or 2 steps)/struggles (for stage 4)
- Score−1: Turns the head back or away
- Score 0: Looks at the person
- Score +1: Approaches the person without touching, sniffs
- Score +2: Approaches and touches the person
- Score +3: Tries to lick/catch the person with the mouth (clothing or hand with the tongue or the lips).

This test was repeated 3 times per cow, with a rest period of at least 5 min between each test period. The mean of each score by stage and by cow was calculated. For example, a frightened cow could score the first time: −2, −2, −3, −2; the second time −1, −2, −3, −3; and the third time: −2, −1, −2, −3: so for each stage the mean for this cow would be: −1.67, −1.67, −2.67, −2.67. For a calm cow, it would be: 0, 0, −1, −1; 0, 0, 1, −1; 0, 0, 0, 0; so the mean would be: 0, 0, 0, −0.67.

Suddenness Test

In winter trial, we tried another test that finally could not be implemented for technical reason; therefore, data were only collected in summer and fall. The aim of this test was to evaluate the reactivity of the cow to a sudden event. Therefore, we dropped an object in front of the target cow and noted the reaction. A white plastic bowling pin (H = 45 cm ø =10 cm) hanging on a fine string was used as a stimulus. The previous evening, the bowling pin were installed above the cows, out of their reach and field of vision. All cows were in a standing position 5 min before the test. The video recording (GoPro®, San Mateo, USA) was started 1.5 min before the start of the test for a 2-min duration, using a camera mounted on tripod in front of the cows (cows were previously habituated to the procedure). After 1.5 min, the manipulator dropped the bowling pin by releasing the string suddenly. He remained approximately two stalls away from the target cow not to disturb the cow. The recording then continued for 30 s (see **Video S2** in Supplementary material).

Using the videos, an observer noted the duration of freezing expressed by the cows (time spent freezing in fixation on the object). The cows were also assigned a reaction score from 0 to 4 according to the following behaviors: No reaction (0); startled, with no backward movement (1); startled, with backward movement of 1 or 2 steps (2); startled, with strong backward movement or taut chain (3); startled, with strong backward movement (with struggle) and taut chain (4).

Statistical Analysis

Winter, summer and fall trials were not designed as replicates but as independent trials to account for large differences in climatic conditions, age of animals, restrictiveness of animal handling, staff availabilities, and responsiveness of animals to flooring conditions and handling methods which were different between trials. Each season was analyzed and reported separately across the manuscript.

We checked the homogeneity of the variance by a Levene test. All data, except the sudden reaction score, was determined to be normally distributed assessed graphically using Q-Q Plot. We implemented a linear mixed-effects model for all scores of human test and for freezing duration in the suddenness test. For the suddenness tests, we implemented a cumulative link mixed-effects model with the reaction score as ordinal variable. For each model, we have considered the following factors:

(1) Phase as a fixed effect: before or after 12-week exercise period
(2) Treatment as fixed effect: Out cows with exercise or NonOut cows without exercise
(3) Phase x Treatment interactions as a fixed effect
(4) Animal nested in pair (pairs formed according to parity and stage of lactation) as a random effect.

Residual normality was visually assessed using a Q-Q plot. *Post-hoc* comparisons were performed by least significant difference (LSD) tests. The threshold of significance was 0.05, and tendencies between 0.1 and 0.05 are mentioned. For the results from the 4 stages of the human test, a Bonferroni correction was applied for multiple comparisons so the threshold of significance considered is $0.05/4 = 0.0125$ and 0.025 for tendencies. Statistical analyses were performed in SPSS 20.0 (®IBM, SPSS Inc., Chicago, Illinois, USA).

RESULTS

Human Test

In winter, the first difference occurred at the third stage with a phase*treatment effect ($F_{3,26} = 7.82$; $P = 0.012$): after the outdoor exercise access period, cows without exercise (NonOut) had the lowest score on the human test (**Table 2**). In the fourth and last stage, we had a phase*treatment effect ($F_{3,26} = 9.93$; $P = 0.004$): after the outdoor exercise access period, Out cows had a higher score compared to before the outdoor exercise access period (LSD, $P = 0.004$), and were less avoidant than NonOut cows (LSD: $P = 0.004$).

In fall, the first difference occurred at the third stage with a phase effect ($F_{1,26} = 10.22$; $P = 0.004$). After the outdoor access period, Out cows had a higher score on the human test compared to before the application of the treatment (LSD: Stage 3: $P = 0.008$; Stage 4: $P = 0.002$; **Table 2**), demonstrating that they approached more and were less avoidant of human stimuli after regular outings.

In the summer, there were no differences between the cows, nor in terms of treatment, phase, or treatment*phase interaction ($P > 0.05$ for all; **Table 2**).

Suddenness Test

In summer, the cows' reactions to a fallen object tended to be different according to treatment*phase ($F_{3,25} = 3.21$; $P = 0.09$). *Post-hoc* comparisons showed that after the outdoor exercise access period, Out cows had a weaker reaction to the fall of the object than NonOut cows (LSD: $P = 0.0001$, **Figure 1A**) and tended to have a weaker reaction than before (LSD: $P = 0.053$). In the fall, a difference was observed between the cows' reactions to a fallen object according to treatment*phase ($F_{3,24} = 4.52$; $P = 0.044$). *Post-hoc* comparisons showed that after the outdoor exercise access period, Out cows had a weaker reaction to the fall of the object than Out cows and NonOut cows before the outdoor exercise access period (LSD: $P = 0.001$), and weaker than NonOut cows after the outdoor exercise access period (LSD: $P = 0.023$, **Figure 1B**).

In summer, the time spent freezing tended to vary depending on the phase ($F_{1,29} = 3.73$; $P = 0.06$): after the outing period, cows tended to spent less time freezing. There was also a tendency for treatment effect ($F_{1,29} = 3.59$; $P = 0.07$): Out cows spent less time freezing than NonOut cows (**Figure 2A**). There were no significant difference according to treatment*phase ($F_{3,27} = 0.66$; $P = 0.42$). In fall, the time spent freezing was different according to phase*treatment ($F_{3,24} = 7.98$; $P = 0.009$). After the outdoor exercise access period, Out cows spent less time freezing than before the treatment period (LSD: $P = 0.021$), and less than NonOut cows (LSD: $P = 0.027$, **Figure 2B**).

DISCUSSION

The results showed, in the summer and fall seasons, that cows provided with outdoor access showed less reactivity to the suddenness test than cows that remained in tie-stalls, without being completely reactionless. Tie-stall cows tethered permanently experience a routine environment throughout the year, since all activity is conducted at the stall. In routine events are consistent, predictable, and not very diversified. While providing outdoor access permits animals to express greater socialization and natural behavior (21, 22), it also means exposing them to initially unknown and diverse stimuli that could heed unforeseeable responses. The provisioning of various stimuli and so, enrichment, allows cows to develop a range of behaviors and reactions, and therefore, promotes the animal's capacities of adaptation (18). This allows the animal to adapt to changes in the environment and assess more quickly the potential for associated risk. They can therefore avoid remaining unnecessarily alert when a sudden stimulus presents itself. It has been demonstrated that the predictability of negative or positive events are very important for animal welfare as it promotes a sense of control (23, 24). On the other hand, too much routine and predictability may support habit formation and prevent animals from developing capacities that would enable them to cope with change. It is therefore important to know how to stimulate animals and their behavior in order to give them more control over disturbing events, which may result in an increased well-being and health. For example, it is possible to use a bell sound to announce the passage of a tractor, or the start of a transfer to the exercise area. Everything that allows the animal to anticipate what will happen will prepare the animal for the event.

Our study shows that cows in the winter trial exposed to outdoor exercise access had a more positive human approach score, especially in the final stages of approach where the human

TABLE 2 | Estimated mean (± S.E.) of cow reactivity scores for each stage of human approach.

Season	Phase	Treatment	Stage 1	Stage 2	Stage 3	Stage 4
Winter	Before	Out	−0.23 ± 0.33	−0.37 ± 0.55	0.11 ± 0.57	−1.21 ± 0.60 **a**
		NonOut	0.22 ± 0.28	0.19 ± 0.47	0.56 ± 0.49	−1.22 ± 0.51 **a**
	After	Out	0.08 ± 0.44	0.34 ± 0.45	0.83 ± 0.38	0.21 ± 0.45 **b**
		NonOut	−0.28 ± 0.43	0.25 ± 0.45	−0.36 ± 0.37	−1.76 ± 0.44 **a**
Fall	Before	Out	−0.33 ± 0.32	0.27 ± 0.57	−1.07 ± 0.36 **a**	−1.67 ± 0.57 **a**
		NonOut	−0.34 ± 0.24	0.11 ± 0.42	−0.63 ± 0.27 **ab**	−1.15 ± 0.42 **ab**
	After	Out	0.07 ± 0.33	0.40 ± 0.51	0.33 ± 0.49 **b**	−0.27 ± 0.52 **b**
		NonOut	0.04 ± 0.24	0.19 ± 0.38	−0.11 ± 0.37 **ab**	−0.78 ± 0.39 **ab**
Summer	Before	Out	−0.38 ± 0.23	−0.49 ± 0.33	−0.07 ± 0.31	−1.88 ± 0.31
		NonOut	−0.08 ± 0.23	−0.21 ± 0.33	−0.38 ± 0.31	−1.63 ± 0.31
	After	Out	−0.39 ± 0.30	−0.04 ± 0.52	−0.72 ± 0.49	−1.10 ± 0.45
		NonOut	−0.71 ± 0.28	−0.71 ± 0.50	−0.58 ± 0.47	−1.63 ± 0.42

Values are displayed separately before and after an outside exercise period (Out) vs. remaining in tie-stalls without an exercise period (NonOut) for each season. Stage 1 represents the most distant position while stage 4 was the most intrusive (when the chain was caught at the neck).

Data represents mean ± S.E. Different letters indicate differences between groups. Post-hoc LSD tests with Bonferroni corrections (significance with $P < 0.0125$).

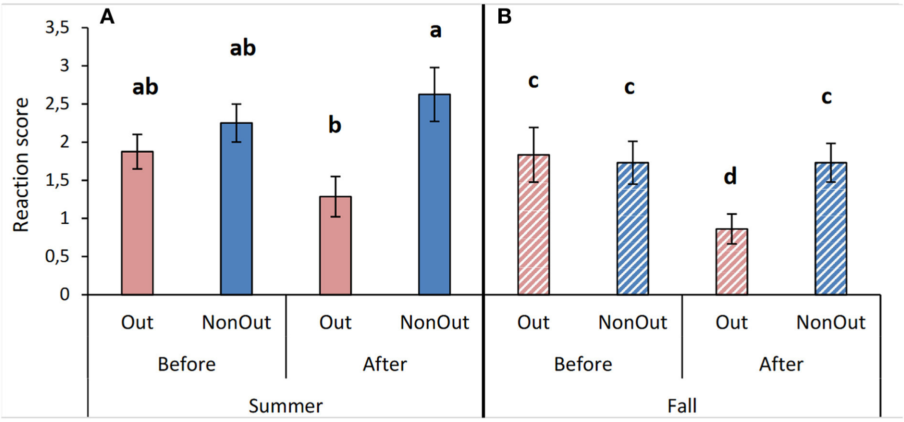

FIGURE 1 | Mean (± S.E.) of cow reaction scores for the suddenness test, measured after dropping an object in front of the cows. Values are displayed before and after an outside exercise period (Out) vs. remaining in tie-stalls without an exercise period (NonOut), for the summer **(A)** and fall seasons **(B)**. Means with the same letter in the same part of the column are not significantly different ($P > 0.05$).

was in closer proximity. As our scoring is done in four steps, it could possibly induce a slight bias. Indeed, the score of a step can be influenced by the score of the previous step: if an animal was already at the end of its stall, it could hardly move further back. However, it is highly likely that the animal will still show backward movement even if it cannot finish it (i.e., do not exit the stall). Thus, this bias would tend to slightly reduce the occurrences of extremely negative scores (scores of −3). This bias is also reduced by the fact that we have averaged the score of 3 repetitions at each step. In conclusion, we believe that the only possible effect of this bias is not to distinguish certain extreme negative cases but does not impact the positive cases. Therefore, a more positive score for cows with access to outdoor space, is probably not affected by this bias to the point of changing the direction of the interpretation of our results. This means that cows could be approached and taken by halters for routine manipulations more easily than cows that did not experience outdoor exercise access. A first potential explanation would be that cows provided with outdoor exercise access became accustomed, over the treatment period, to being regularly handled. As such, the response of fear and avoidance toward handling would have decreased as shown in other studies (25, 26). However, this effect was not present for the summer trial, since cows with outdoor exercise access had an approach score that was not different, regardless of approach stage, from cows that remained at their tie-stall. We may therefore conclude that the results were not explained by a simple habituation toward the handling process.

A second potential explanation would be that the sample group of cows observed in the summer trial were more fearful than cows observed in the winter trial, thus masking the effect of habituation to the handling process. Indeed, by reacting more to a human movement, which could take the animal by surprise, cows could show more fearful behaviors toward a human stimulus. However, we have observed that cows provided with outdoor access in the summer trial were less reactive after the treatment

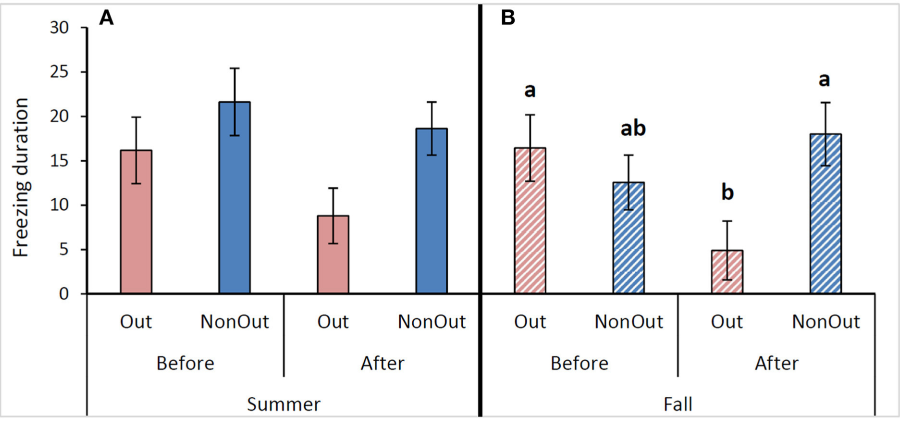

FIGURE 2 | Mean (± S.E.) of freezing duration (s) for the suddenness test, measured after dropping the object in front of the cows. Values are displayed before and after an outside exercise period (Out) vs. remaining in tie-stalls without an exercise period (NonOut), for the summer **(A)** and fall seasons **(B)**. Means with different letters are significantly different ($P < 0.05$).

period than cows that remained in their stall. Thus, a simple cross effect between fear and habituation of handling/human cannot explain the results obtained. The observed effect may be directly linked to the valence of the relationship between animals and humans.

The attachment of the halter for these tie-stall cows is an event generally associated to be negative, since this occurs rarely and most often for changing stalls or medical attention. It is a disruption of daily routine, a restriction of access to resources such as feed or lying, and may potentially be associated with painful veterinary care. As part of the handling procedure for leading cows to the outdoor exercise area, halters were put on to secure the cow's removal from the stall. We could therefore conclude that cows provided with outdoor exercise access associated the halter with a predictable positive event, and subsequently, were more accepting and easily handled at the neck (the halter level). This was observed for the winter but not for the summer trial. It has already been shown that cows are sensitive to the way they are handled (11), and that aversive manipulations modify their relationship with humans (27). Cows are even able to discriminate between people based on their past experiences with them, and thus may react positively or negatively to their contact (10, 28, 29). One of the main differences between the summer and winter trials is that, in winter, the cows moved freely in the outside corridor and the handlers only intervened to push them when they stopped moving for too long during this part of the trip. In the summer, on the other hand, the cows were more excited and made many attempts to run. In order to avoid injuries to both the cows and humans, handlers were also placed in front of the cows to regularly calm them and stop them from running with halter. In the fall, there were someone in the front to help to stop the cows when running, but were more inclined to let the cows move faster/run a little in some occasions if no possible danger was assessed. In the summer, cows were more regularly caught at the halter to restrict their movements. Presumably, their movement was more restricted, and so the handling could have been perceived in a more negative way compared to cows who moved freely in the winter trial. We cannot assume that cows perceived the handling aversively, since they did not show a more negative approach score than the control cows, but they likely did not perceive the experience in a positive way. We thus conclude that cows provided with outdoor exercise access during the winter trial have an altered and more positive perception of the halter placement, while the summer Out cows perceived the halter more negatively. It should be emphasized that the motivation of cows to go outdoors was very apparent in both the summer and winter trials (Aigueperse et al. in prep), but the association of a negative event, particularly a strong one, will often impact behavior more heavily than a positive event (28, 30).

In conclusion, our study shows that the provision of regular outdoor access to tie-stall cows may therefore reduce reactivity under certain conditions. If we assume that this was an effect of providing stimuli linked to the varied conditions of the external environment, the exact mechanisms involved in changes to reactivity require further investigation. In addition, we showed that cow handling during these outings also had an impact on the cow's relationship with humans, and therefore on their future ease of handling. The provisioning of regular exercise for tie-stall cows is seen as a source of enrichment and improvement of quality of life in animals (31–33). To demonstrate the positive effect of this practice, many factors must be considered, including its impact on the health and locomotor capacities of the animals, how enrichment is provided (i.e., type of access, space, etc.), but also the handling of animals during the process. All of these factors may affect the behavior of cows, and their perception of the experience and so, have an impact on their well-being. Proper handling taking in consideration the cow's reactivity and experience gained from multiple handling sessions can improve the behavior and perception of animals. In addition, it can improve the well-being of the handler through more safety, a better relationship with their animal and a better vision of their work.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Animal Care Committee of McGill University and affiliated hospitals and research institutes (protocol #2016-7794).

AUTHOR CONTRIBUTIONS

NA and EV designed the study. NA performed the experiments and analyzed the data. NA wrote the original draft of the article and all the author finalized the final version. EV provided funding. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2020.597607/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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'Puppy Dog Eyes' Are Associated With Eye Movements, Not Communication

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The inner brow raiser is a muscle movement that increases the size of the orbital cavity, leading to the appearance of so-called 'puppy dog eyes'. In domestic dogs, this expression was suggested to be enhanced by artificial selection and to play an important role in the dog-human relationship. Production of the inner brow raiser has been shown to be sensitive to the attentive stance of a human, suggesting a possible communicative function. However, it has not yet been examined whether it is sensitive to human presence. In the current study, we aimed to test whether the inner brow raiser differs depending on the presence or absence of an observer. We used two versions of a paradigm in an equivalent experimental setting in which dogs were trained to expect a reward; however, the presence/absence of a person in the test apparatus was varied. In the social context, a human facing the dog delivered the reward; in the non-social context, reward delivery was automatized. If the inner brow raiser has a communicative function and dogs adjust its expression to an audience, we expect it to be shown more frequently in the social context (when facing a person in the apparatus) than in the non-social context (when facing the apparatus without a person inside). The frequency of the inner brow raiser differed between the two contexts, but contrary to the prediction, it was shown more frequently in the non-social context. We further demonstrate that the inner brow raiser is strongly associated with eye movements and occurs independently in only 6% of cases. This result challenges the hypothesis that the inner brow raiser has a communicative function in dog-human interactions and suggests a lower-level explanation for its production, namely an association with eye movements.

Keywords: dog, DogFACS, facial expressions, inner brow raiser, AU101, puppy dog eyes, social use, signal

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INTRODUCTION

Facial expressions accompany (putative) emotional states in humans and non-human animals (reviewed by Descovich et al., 2017) and can provide information about an individual's intentions and potential future behavior (Waller et al., 2017), both in positive contexts such as signaling playful intent (Fox, 1970) and in negative contexts such as predicting aggression (Camerlink et al., 2018). While facial expressions have often been considered to be mainly reflexive and invariable, particularly when linked to emotional states (see e.g., Liebal et al., 2014; Scheider et al., 2016; reviewed by Jones et al., 1991; Kaminski et al., 2017), for humans and several non-human primate species there is evidence of *audience effects* on the production of facial expressions: individuals will adjust their facial displays depending on the presence or attentive state of an observer (e.g., Kraut and Johnston, 1979; Jones et al., 1991; Liebal et al., 2004; Poss et al., 2006; Demuru et al., 2015; Waller et al., 2015; Scheider et al., 2016). This sensitivity to an audience suggests a communicative function of the respective expression (Leavens et al., 1996), which may thus constitute a '*signal*,' i.e., a behavior evolved for the purpose of information conveyance (Laidre and Johnstone, 2013). In contrast, a '*cue*' constitutes a mere by-product of an animal's behavior which may coincidentally convey information to another individual (Shariff and Tracy, 2011; Laidre and Johnstone, 2013). The only non-primate species where the effect of an audience on the production of facial expressions has so far been reported, to our knowledge, is the domestic dog (*Canis familiaris*) (Kaminski et al., 2017).

To assess whether human attention and/or an emotionally arousing stimulus affected facial expressions in dogs, Kaminski et al. (2017) compared dogs' facial expressions directed at either an attentive person (standing in front of and facing the dog) or an inattentive person (turned away from the dog). Additionally, it was varied whether or not this person was holding a piece of food (considered to be an emotionally arousing stimulus) (Kaminski et al., 2017). In line with an audience effect, dogs' facial expressions differed depending on the person's attentive stance, and this effect was particularly strong for two actions: the 'inner brow raiser' and 'tongue show,' which were shown more often when the human was facing the dog than when she was turned away, implying a possible communicative function of these expressions (Kaminski et al., 2017). The visibility of the food item, however, did not significantly affect the dogs' facial display, suggesting that it does not primarily constitute an emotional expression (Kaminski et al., 2017).

The inner brow raiser in particular has attracted researchers' attention in the context of dog-human communication. By raising the medial part of the eyebrow, the inner brow raiser increases the height of the orbital cavity, thus creating the impression of larger eyes (Waller et al., 2013). This paedomorphic expression was hypothesized to be particularly attractive to humans (Waller et al., 2013). One study reported that in shelter dogs, the rate of the inner brow raiser (measured when a person was standing in front of the kennel) was inversely related to time at the shelter until rehoming (Waller et al., 2013). Dogs with a high frequency of raising the brow might thus have a selective advantage (Waller et al., 2013). This effect may not only be at work in the current environment, but by using rehoming speed as a proxy for human selection during evolution, it was proposed that performance of the inner brow raiser was selected for in dogs in the course of domestication (Waller et al., 2013).

To investigate this hypothesis further, Kaminski et al. (2019) compared the production of the inner brow raiser as well as anatomical features underlying this movement in dogs and their closest extant relatives, gray wolves (*Canis lupus*). The study indicated differences between the species in both anatomy and behavior: in dissections of six domestic dogs and four wolves, the muscle responsible for the inner brow raiser movement (*levator anguli oculi medialis* = LAOM) was typically pronounced in dogs, whereas in the wolves it was more variable, usually ill-defined and not a separate muscle (Kaminski et al., 2019). Kaminski et al. (2019) further compared the production of inner brow raiser movements in shelter dogs and captive gray wolves when a human observer was standing in front of the kennel/enclosure. A higher frequency and intensity of inner brow raiser movements were observed in the dogs compared to the wolves (Kaminski et al., 2019). Thus, Kaminski et al. (2019) concluded that artificial selection resulted in a change in the facial musculature of dogs to enhance dog-human communication.

If a behavior has a communicative function, it would be expected to vary contextually based on the presence or absence of a receiver of this expression. For example, chimpanzees were considered to use a behavioral action communicatively if it was shown more often when a human observer was present than in the absence of an audience (Leavens et al., 1996). However, this most basic form of an audience effect, namely whether dogs' production of the inner brow raiser is affected by the presence of an audience (also referred to as social use, see Liebal et al., 2014; Waller et al., 2015), has not been tested so far.

Our first aim, therefore, was to investigate whether the inner brow raiser in dogs is sensitive to the presence of an audience. To this end, we compared dogs' expression of the inner brow raiser in a social context with an interacting human and in a non-social context without face-to-face interaction with a human. Using a within-subjects design, dogs were trained to expect a reward from an apparatus where the reward was delivered either (1) through a remotely controlled reward-delivery system without a person inside the apparatus (non-social context) or (2) by a person sitting inside the apparatus and facing the dog (social context). The social context represented a situation in which dogs were expected to likely communicate with humans, namely when awaiting a reward to be delivered by a person (Gaunet, 2008, 2010). In addition, we varied other situational features and explored their effect on the inner brow raiser production to enhance the validity of our findings. Therefore, in both the non-social and the social context we also varied the valence of the trial (positive: anticipation of a reward; negative: prevention of access to a visible reward) and the reward type the dogs were conditioned to expect. We used food and toys as both are considered to function as rewards in dogs (Gerencsér et al., 2018). However, they can be associated with different appetitive behavioral actions (i.e., ingestion of a palatable item vs. object manipulation), motivational states (e.g., Burghardt et al., 2016), and individual responsiveness (Gerencsér et al., 2018). Based on the previous evidence that the inner brow raiser serves a communicative function (Kaminski et al., 2017), but does not reflect an emotional state (Caeiro et al., 2017; Kaminski et al., 2017; Bremhorst et al., 2019), we predicted a higher incidence of the inner brow raiser in the social context (when facing a human) than in the non-social context, but no effect of trial valence.

Our second aim concerned the proximate mechanisms of the inner brow raiser movement. We explored an alternative hypothesis for its production in different contexts, given that the principle of parsimony postulates that lower-level explanations have to be ruled out before drawing conclusions regarding cognitively more complex processes (see Epstein, 1984; Zentall, 2017). According to the manual on DogFACS (Waller et al., 2013), an anatomically based coding method to systematically identify facial appearance changes due to muscle movements in dogs, the inner brow raiser appears to accompany eye movements and can even be used to infer eye movements, which are sometimes hard to detect. However, if the inner brow raiser primarily accompanies eye movements, then differences in its production between contexts could be an artifact simply based on differences in gazing behavior, providing a possible lower-level explanation for observations of this facial expression. Empirical evidence for an association between the inner brow raiser and eye movements is lacking. Therefore, in a subsequent second step, we used the video samples generated for our first research aim to analyze the frequency of eye movements across the different contexts and their association with the inner brow raiser.

MATERIALS AND METHODS

Subjects

Our subjects were 21 family pet dogs (12 females and 9 males; mean age: 4.76 years ± *SD* = 2.77; see **Supplementary Table 1** for details), recruited personally or via social media. To minimize effects of morphological variation on the facial display, we included only one breed without morphological extremes, Labrador retrievers, and one Labrador cross with a Labrador-like morphology.

Study Design

The study consisted of two versions of a paradigm with an equivalent experimental setting and contingencies, except that a person was either absent (non-social context) or present (social context) inside a test apparatus (**Figure 1**). The dogs were conditioned to expect a desired reward (toy/food) to be delivered from this test apparatus. In the non-social context, the reward was delivered remotely. In contrast, in the social context, the experimenter was sitting inside the apparatus, visible to the dog, and handed the reward to the dog.

The following test conditions were varied (**Figure 2**): (1) context – non-social and social (absence or presence of a person inside the test apparatus), (2) reward type – toy and food, and (3) valence of the trial – positive (anticipation of access to a reward) and negative (prevention of access to a visible reward).

Test Apparatus

The test apparatus was a custom-made wooden/metal construction (1.80 × 0.90 m) with a delivery window approximately at the dogs' head height. The window could be covered using a remote-controlled transparent Perspex panel, which allowed for the filming of the dogs' facial expressions while they were waiting for the reward. In the social context, a piece of cardboard was additionally used to cover the window to prevent the dogs from seeing the experimenter between trials. The interior of the apparatus varied between the non-social and the social context. In the non-social context, an automatic reward dispenser (functioning like a trap door) onto which the reward could be placed was mounted in the apparatus above the dog's head height (**Figure 1**). The reward dispenser was hidden behind a piece of cloth to prevent the dogs from seeing the reward before it was delivered. In the social context, a wooden table was mounted in the apparatus and connected to the window. The experimenter sat in the apparatus so that her head was at approximately the same height as the reward dispenser in the non-social context (**Figure 1**).

Experimental Procedure

Preliminary Preference Tests

With each dog, we conducted preference tests first between two toys and then between two food types, using paired presentations over 10 trials per reward type. As we only wanted to use rewards that the individual was motivated to obtain, the respective reward type was used for testing if the dog made a choice in at least eight trials, and the more frequently selected option was used in the subsequent procedure. All 21 dogs met this criterion with the food reward and 19 dogs with the toy reward. The 19 dogs that were sufficiently motivated for both reward types were additionally tested in a third preference test in which they could choose between their most preferred food and their most preferred toy over 10 trials. As all but two dogs preferred the food to the toy reward, this factor was not considered in the subsequent analyses.

Training

Training trials served to condition the dogs to approach the apparatus and to wait for 5 s until the reward was delivered. At the start of each trial, the window of the apparatus was covered by the Perspex panel and in the social context by the additional piece of cardboard. The owner was sitting on a chair 1.80 m from the apparatus with the dog next to her or him. The owner then released the dog and gave a verbal and visual release signal. In the first trials of the session (five trials in the first training session; in case a second training session was required, this was reduced to three), the owner then walked to the front of the apparatus and looked into it to draw the dog's attention to this location. In all other trials, the owner remained sitting on the chair, which allowed us to see whether the dog approached the apparatus on her/his own, indicating the subject's motivation and level of training to associate the apparatus with the reward. After 5 s, regardless of the dog's behavior, the transparent panel was slid upwards by means of a remote-controlled system and the reward (which until then was out of the dog's view) was delivered.

In the non-social context, reward delivery was performed by the automated system, i.e., as soon as the trap door was activated remotely, the reward fell onto a slide and slid down to the window, where it became accessible to the dog. In the social context, delivery was performed by the experimenter who handed the reward (which she had been holding in her hand below the wooden table) to the dog through the window. The dog could

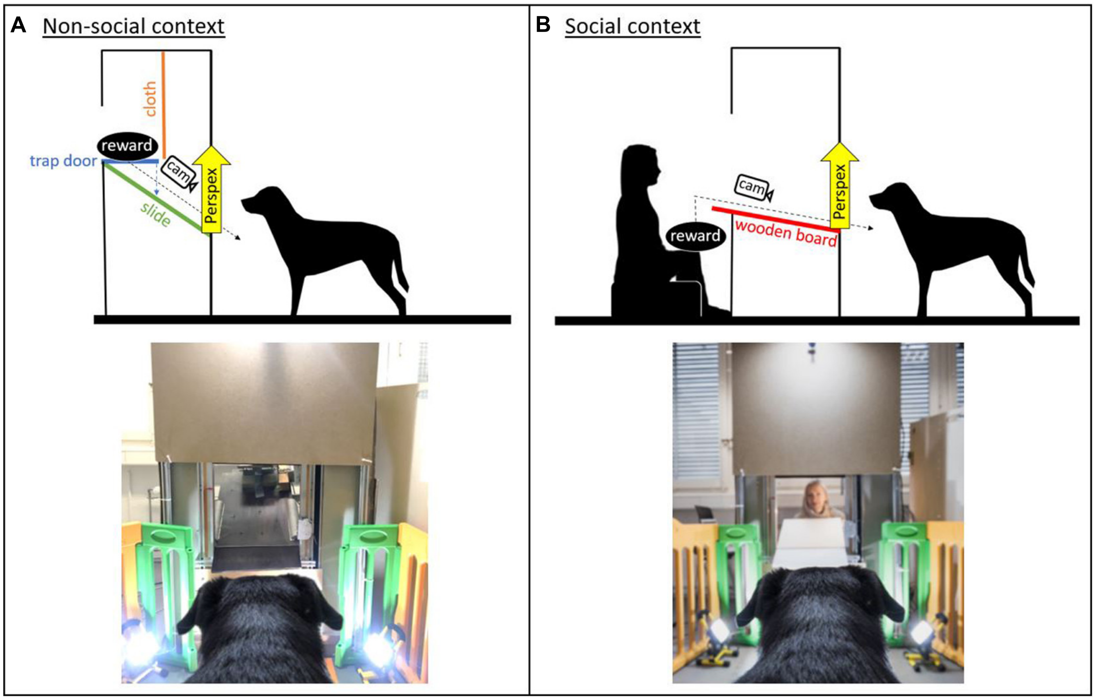
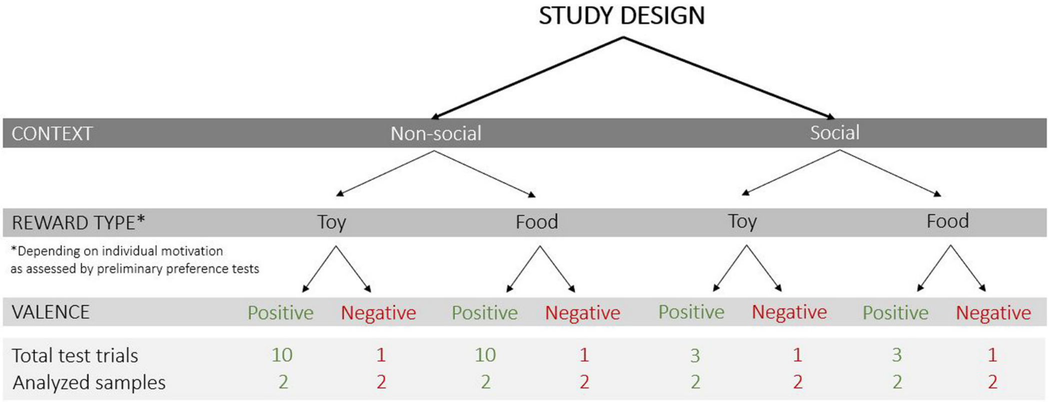


FIGURE 1 | Sketch of the experimental set-up and image of the apparatus in the **(A)** non-social context and **(B)** social context (with the experimenter present inside the apparatus; image credit: Adrian Bear/Tierwelt).



CONTEXT	Non-social				Social			
REWARD TYPE*	Toy		Food		Toy		Food	
VALENCE	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative
Total test trials	10	1	10	1	3	1	3	1
Analyzed samples	2	2	2	2	2	2	2	2

FIGURE 2 | Study design with the test conditions that varied in the current study (context: non-social/social; reward type: toy/food; valence of the trial: positive/negative), the total number of test trials and analyzed samples (each sample was a 3 s video clip).

then consume the reward (ingest the food or play with the toy for a maximum of 30 s; this duration varied between individuals mainly due to differences in interest, play behavior, strength of motivation, obedience when returning the toy, etc.). At the end of each trial, the transparent panel was remotely activated to move down until it completely covered the window again. The next trial commenced shortly after the dog was back in the starting position next to the owner.

The training criterion to proceed to the test was that the dog immediately approached the apparatus on her or his own when released and waited in front of the apparatus until the reward was delivered in five consecutive trials. Only trials in which the owner remained sitting were evaluated for this purpose. This training criterion provided an objective means to evaluate the dog's association between the apparatus and the reward and allowed to consider individual learning speed while keeping the number of repetitions as low as possible to avoid loss of interest.

A maximum of two training sessions with 10 trials each was conducted. If the dog did not reach the training criterion within these sessions, or if motivation decreased over repeated trials (i.e., the response deteriorated), training was terminated with this reward type in the respective context. The 19 dogs who were sufficiently toy motivated in the preference test were first trained with their preferred toy reward (and second with food) in both the non-social and the social context. Of these, 12 dogs reached the training criterion and were tested with the toy reward in the non-social context. In the social context, 15 dogs passed the training criterion and proceeded to testing with the toy (see **Supplementary Table 1** for an overview). All 21 subjects were sufficiently motivated for the food reward in the preference test, reached the training criterion within two sessions in both the social and the non-social context and were therefore tested with food rewards in both contexts.

Testing

Positive and negative test trials were conducted (video examples of a positive and a negative test trial in the social and the non-social context are provided as **supplementary material**). The procedure of the positive test trials was the same as in the training trials (described in section 'Training'), with the 5 s delay until reward delivery considered as the 'anticipation phase'. In the negative test trials, the reward was also delivered after 5 s, but the transparent panel did not open for 60 s (i.e., the 'frustration phase'). During this time, the dog could see the reward lying in front of the transparent panel in the apparatus (non-social context), or in the experimenter's hand (social context), but was unable to obtain it.

In trials of the social context (both training and testing), the experimenter always sought eye contact with the dog (without continuous direct staring) to facilitate a natural communicative interaction. The experimenter's facial expression was friendly with a gentle smile to avoid any reluctance of the dogs to approach, which could be the case with a neutral face, as a neutral expression seems to be interpreted negatively by dogs (Racca et al., 2012; Ford et al., 2019).

All dogs first participated in the non-social context and subsequently in the social context. The fixed order of contexts was selected for reasons relating to project management and because we did not want to create an expectation of the experimenter handing the reward to the dog (as done in the social context) before the dog was tested in the non-social context. This might have attracted the dog's focus away from the apparatus to the experimenter, who was also in the room during the non-social context (hidden behind a divider behind the dog) to operate the apparatus. Furthermore, the dogs always participated in the toy condition first, if applicable, as pilot studies had shown that loss of interest could be prevented by performing the session with the reward type that was preferred by nearly all subjects (food) after the session with the less preferred toy reward.

As a result of the fixed order of contexts, fewer training trials were required for the social context than for the non-social context, presumably because the dogs were already familiar with the procedure and the apparatus (mean number of evaluated trials until the training criterion was reached: non-social context—toy: 8.58, food: 5.33; social context—toy: 5.00, food: 5.00). Consequently, whereas in the non-social context training and testing of each reward type was performed in separate sessions to keep the number of repetitions low and prevent fatigue, in the social context training and testing could be combined in one session.

In the non-social context, five positive test trials were conducted before a single negative test trial. Five additional positive trials performed subsequently were aimed at reducing potential carry-over effects of this negative experience on the performance in the subsequent social context, although in the meantime we found that valence of the preceding trial does not seem to considerably affect expressions in the subsequent trial (Bremhorst et al., 2019). In the social context, two positive test trials were conducted directly after the training criterion was reached, followed by a single negative trial. A last positive test trial was aimed at ending the study with a positive experience for both the dog and the owner.

Behavior Coding

Preparation of Video Samples

For each of the 21 subjects, two positive and two negative video samples of 3 s duration per reward type (food/toy when applicable) were created for each context (non-social/social). The duration of the samples was determined by the length of the positive trials; from the two positive trials directly preceding the negative trial, we used the middle 3 s from the 'anticipation phase' (i.e., ending 1 s before the transparent panel started to open). A previous study has shown that this time interval is long enough for several facial movements to occur (Bremhorst et al., 2019). For comparability, negative samples were of equal quantity and length as the positive samples, i.e., following the procedure of Bremhorst et al. (2019), two randomly selected negative samples of 3 s duration each were cut from the 'frustration phase' of the negative trial (excluding the first 10 s as the frustration response may not be triggered immediately).

A total of 276 samples was prepared, comprising 132 samples from the non-social context (toy positive: 24 samples, toy negative: 24 samples, both $N = 12$ (N refers to the number of subjects); food positive: 42 samples, food negative: 42 samples, both $N = 21$) and 144 samples from the social context (toy positive: 30 samples, toy negative: 30 samples, both $N = 15$; food positive: 42 samples, food negative: 42 samples, both $N = 21$).

Inner Brow Raiser Coding

Using DogFACS (Waller et al., 2013[1]), coding of the inner brow raiser (which is labeled with the code AU101) was performed (see **Figure 3** for an example of a bilateral inner brow raiser). As a first step, the frequency of the inner brow raiser in the 276 samples was coded by two certified DogFACS coders, one of whom was blind to the research hypothesis. As is common practice to the authors' knowledge, the inner brow raiser was coded independently of eye movements. Reliability between the coders over the 276 samples was very good with an average intraclass correlation coefficient of 0.80 (95% CI: 0.72–0.85).

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[1] www.animalfacs.com

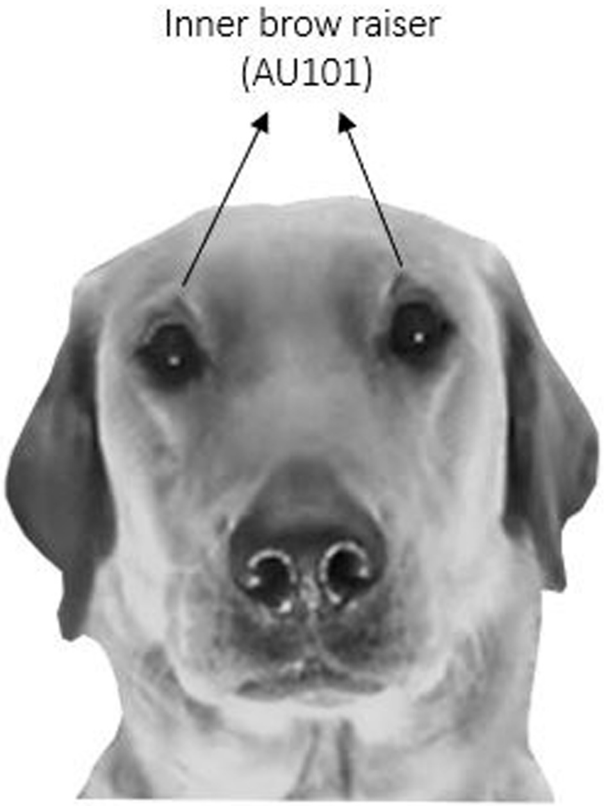

FIGURE 3 | Dog producing a bilateral inner brow raiser movement.

Eye Movements and Combinations With the Inner Brow Raiser Coding

In a second step, we subsequently coded eye movements in four directions [left, right, up, down; as described in the DogFACS manual (Waller et al., 2013)]. To analyze the association between eye movements and the inner brow raiser, the following combinations of both behaviors were furthermore recorded: eye movements occurring (1) simultaneously (i.e., within 0.2 s) with the inner brow raiser ('Eye movement present/inner brow raiser (*movement*) present'), (2) while the inner brow raiser remained tensed ('Eye movement present/inner brow raiser (*tension*) present'), (3) without inner brow raiser movement or tension ('Eye movement present/inner brow raiser absent'), or (4) inner brow raiser movement occurring without eye movement ('Eye movement absent/inner brow raiser present').

Coding was performed by a certified DogFACS coder who was blind to the research hypothesis, using a subsample of the original video samples. For this subsample, one positive and one negative sample per reward type from both the social and the non-social context were initially selected for each subject. We equally balanced between subjects whether the first or second of the two samples of each valence was used. However, if eye movement was hard to detect in the selected sample (mainly due to environmental conditions such as bad lighting or video quality such as insufficient sharpness), it was excluded from the analysis and the second sample of the corresponding condition was used if the eye movements were clearly detectable. It was not possible to obtain usable samples from all dogs from all conditions due to a lack of image quality; therefore the final subsample comprised 95 samples including 50 samples from the non-social context (toy positive: 10 samples, $N = 10$; toy negative: 11 samples, $N = 11$; food positive: 17 samples, $N = 17$; food negative: 12 samples, $N = 12$) and 45 samples from the social context (toy positive: 10 samples, $N = 10$; toy negative: 7 samples, $N = 7$; food positive: 14 samples, $N = 14$, food negative: 14 samples, $N = 14$). From each of the 21 individuals, at least one sample was included in the subsample.

To analyze intercoder reliability, a second certified DogFACS coder coded 20 of these samples (>20% of all videos of the subsample; 10 samples each were randomly selected from the social and the non-social context). Reliability between the two coders was very good with an average intraclass correlation coefficient of 0.93 (95% CI: 0.82–0.97) for 'Eye movement present/inner brow raiser (*movement*) present' and 0.89 (95% CI: 0.71–0.96) for 'Eye movement present/inner brow raiser (*tension*) present'. There was a complete agreement for 'Eye movement present/inner brow raiser absent' and 'Eye movement absent/inner brow raiser present'.

Statistical Analyses

Statistical analyses were conducted in R Studio (version 1.2.1335).

Inner Brow Raiser

We analyzed whether the frequency of the inner brow raiser was affected by the test conditions that varied in the current study (context, reward type, valence of the trial) and by subject sex and age. Linear mixed effect models were computed (function: lme; package: nlme), using the frequency of the inner brow raiser as a response variable. Context (non-social/social), reward type (toy/food), valence of the trial (positive/negative), subject sex (female/male), and age were used as predictor variables. Subject ID was included as a random factor. Model assumptions were verified using visual inspection of the residuals.

To evaluate whether there was a relationship between the inner brow raiser and sample order within the social or the non-social context, we correlated the frequency of the inner brow raiser within each context with the sample number, using a repeated measures correlation (function: rmcorr; package: rmcorr; Bakdash and Marusich, 2017). When both reward types were tested within a context, the sample number ranged from one to eight; when only food was tested, it ranged from one to four.

Eye Movements and Combinations With the Inner Brow Raiser

To analyze whether the frequency of eye movements differed between the non-social and the social context and was affected by reward type, valence of the trial, subject sex, or age, linear mixed effect models were computed using the same approach as previously described for the inner brow raiser (section 'Inner Brow Raiser').

Associations between the inner brow raiser and eye movements were analyzed descriptively by comparing the frequencies of 'Eye movement present/inner brow raiser (*movement*) present', 'Eye movement present/inner brow raiser (*tension*) present', 'Eye movement present/inner brow raiser absent', and 'Eye movement absent/inner brow raiser present', and inferentially by computing a Cochran-Mantel-Haenszel chi-square test (function: cmh_test, package: coin). The four quadrants used for this test were the frequencies of events in which eye movements and/or the inner brow raiser were observed ('Eye movement present/inner brow raiser present (*movement* and *tension* summarized)', 'Eye movement present/inner brow raiser absent', 'Eye movement absent/inner brow raiser present') as well as 'Eye movement absent/inner brow raiser absent'.

RESULTS

Inner Brow Raiser

Context (non-social/social) was the only predictor that significantly affected the inner brow raiser production: the inner brow raiser was shown more frequently in the non-social context than in the social context [$F_{(1,\ 252)} = 24.62$, $P < 0.0001$; $N = 21$; see **Table 1** and **Figure 4**]. Neither reward type nor valence of the trial, subject sex, or age affected the frequency of the inner brow raiser significantly (**Table 1**).

The frequency of the inner brow raiser was unrelated to sample order both within the non-social context (repeated measures correlation $r_{\mathrm{rm}} = 0.02$; $P = 0.87$; 95% CI: −0.17 to 0.20; $N = 21$) and the social context (repeated measures correlation $r_{\mathrm{rm}} = -0.11$; $P = 0.23$; 95% CI: −0.28 to 0.07; $N = 21$).

Eye Movements and Combinations With the Inner Brow Raiser

As with the inner brow raiser, eye movements were significantly affected only by context: eye movements were produced more frequently in the non-social context than in the social context [$F_{(1,\ 71)} = 5.23$, $P = 0.03$; $N = 21$]. There was no significant effect of reward type, trial valence, subject sex, or age (**Table 2**).

Across all 211 observations of the inner brow raiser and/or eye movements, in 94% of cases (198 of 211 observations) eye movements occurred in conjunction with an inner brow raiser movement or inner brow raiser tension. In 63% (132 observations), the inner brow raiser movement was simultaneous with eye movements and in 31% (66 observations) the brows remained tensed while the eyes were moving (**Figure 5**). Eye movements were never observed without the inner brow raiser, and the inner brow raiser without eye movements was only observed in 6% of cases (13 observations; **Figure 5**).

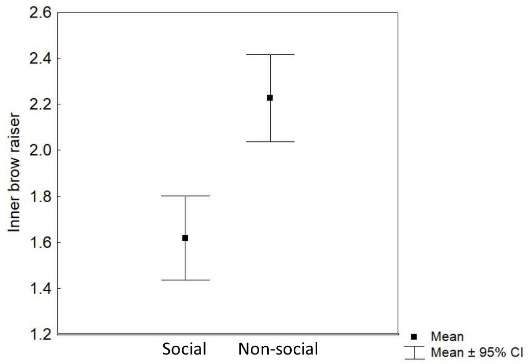

FIGURE 4 | Mean and 95% confidence interval of the frequency of inner brow raiser movements per 3 s video sample in the social and the non-social context.

TABLE 2 | Results of the linear mixed effect model with eye movements as a response variable and context (social/non-social), reward type (toy/food), valence of the trial (positive/negative), subject sex (female/male), and age as predictor variables.

	Eye movements			
Predictor	***df***	***F***	***P***	**95% CI**
Context	**1, 71**	**5.23**	**0.03**	**−1.24 to −0.10**
Reward type	1, 71	0.01	0.91	−0.58 to 0.61
Valence of the trial	1, 71	0.07	0.79	−0.49 to 0.62
Sex	1, 18	0.16	0.69	−0.59 to 0.90
Age	1, 18	0.004	0.95	−0.14 to 0.15

TABLE 1 | Results of the linear mixed effect model with the inner brow raiser as a response variable and context (social/non-social), reward type (toy/food), valence of the trial (positive/negative), subject sex (female/male), and age as predictor variables.

	Inner brow raiser			
Predictor	***df***	***F***	***P***	**95% CI**
Context	**1, 252**	**24.62**	**<0.0001**	**−0.89 to −0.39**
Reward type	1, 252	0.17	0.68	−0.22 to 0.31
Valence of the trial	1, 252	0.40	0.53	−0.33 to 0.17
Sex	1, 18	0.22	0.65	−0.59 to 0.28
Age	1, 18	0.92	0.35	−0.12 to 0.04

The quadrant 'Eye movement absent/inner brow raiser absent' was calculated by first computing the maximum possible frequency of codable events in the subsample (consisting of 95 samples). In each sample (3 s duration), a maximum of 15 events could be coded (i.e., one event per observation unit of 0.2 s). From the resulting maximally codable 1,425 events in the subsample (i.e., 95 samples × 15 events), the frequencies of the coded events of each behavior combination were subtracted to obtain the frequency of events (0.2 s units) in which no eye movement or inner brow raiser was initiated (see **Table 3**). The association between the inner brow raiser and eye movements was highly significant ($\chi^2_{\mathrm{MH}} = 1322.1$, $df = 1$, $P < 0.0001$; $N = 21$).

DISCUSSION

Dogs' expression of the inner brow raiser differed significantly between the non-social and the social context; however, contrary

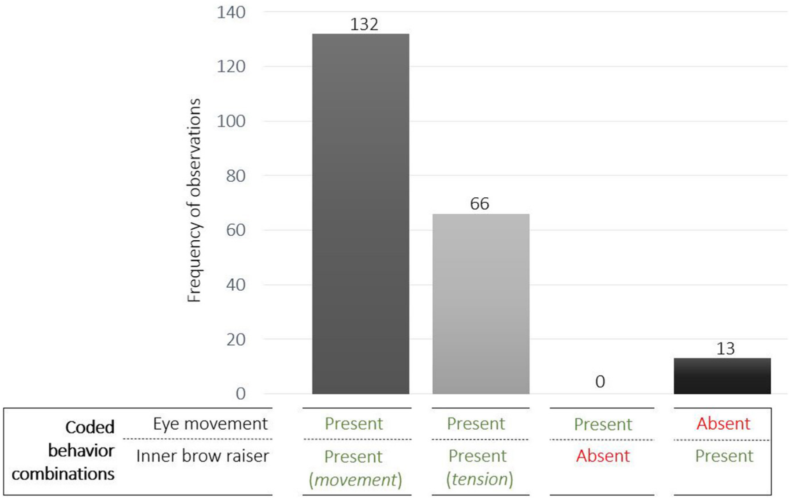

FIGURE 5 | Frequency of observations of the coded behavior combinations of eye movements and/or the inner brow raiser.

TABLE 3 | 2 × 2 contingency table showing the four quadrants used for the Cochran-Mantel-Haenszel chi-square test, based on 95 video samples with 15 events each, resulting in a total of 1,425 events.

		Eye movement	
		Present	**Absent**
Inner brow raiser	**Present**	198 (*movement* + *tension*)	13
	Absent	0	1,214

to the prediction, dogs performed the inner brow raiser more frequently in the non-social context, regardless of the expected reward type, trial valence, subject sex, or age. This direction of effect challenges the assumption that the inner brow raiser is used functionally by dogs for communication with humans (see Kaminski et al., 2017, 2019), and alternative explanations for the production of the inner brow raiser need to be considered.

Our results demonstrate that the inner brow raiser rarely occurs on its own but is usually shown in conjunction with eye movements. Likewise, eye movements were never observed without either the inner brow moving simultaneously or remaining tensed. Thus, the inner brow raiser appears to be an integral feature of eye movements. Consequently, the most likely explanation for the effects of the sociality of the context on the production of the inner brow raiser is the difference in gazing behavior between the social and the non-social context.

Several factors can potentially account for the lower frequency of gaze changes (and thus inner brow raiser movements) in the social context. As dogs are prone to looking at humans' faces (Miklósi et al., 2003), in particular the eye area (Topál et al., 2014), the experimenter's face was likely a highly salient stimulus for them to focus on. Furthermore, eye contact in a face-to-face setting, as it was the case in the social context, was described to increase dogs' attention to a human's face (Topál et al., 2014). Conversely, without a face to focus on, the dogs may have been looking around more in the non-social context. Importantly, as the experimenter was seated on a low stool in the current study, looking into her face (like looking at the automatic reward dispenser) did not require the dogs to move their eyes much – unlike in previous studies where the experimenters were standing (Waller et al., 2013; Kaminski et al., 2017, 2019) and the dogs would presumably have to look up to make eye-contact.

Another factor that could potentially have differed between the two contexts is the state of arousal. Arousal, which could be triggered by the proximity or orientation of another individual, has been considered a potential (lower-level) mechanism for audience effects (Zajonc, 1965; Liebal et al., 2014). In the current study, high arousal might be associated with greater vigilance and thus increased rates of eye movements and consequently brow movements. It could be hypothesized that dogs' arousal declined over the course of the testing sessions (first the non-social context, then the social context) due to dogs habituating to the set-up and procedure. However, if arousal was driving the differences between contexts, we would also expect it to operate within each context, and the same should apply to arousal during the tests with different reward types (with the toy condition always preceding the food condition). The fact that there was no significant effect of reward type on the inner brow raiser argues against differential arousal levels as the decisive factor. Likewise, sample order did not have a significant effect on the production of the inner brow raiser. To better understand the effect of arousal on eye and inner brow movements, future studies could additionally collect physiological parameters that indicate a subject's arousal level, such as heart rate (e.g., Zupan et al., 2016), eye or ear temperature (e.g., Riemer et al., 2016; Travain et al., 2016).

In the current study, we have demonstrated that the inner brow raiser is primarily incidental to eye movements in dogs and presumably not of general communicative value. The finding highlights the importance of considering simpler mechanisms before inferring cognitively more complex interpretations, as also recently discussed for the study of canine emotions (Zentall, 2017). We suggest that the previous findings on the possible social function of the inner brow raiser (Kaminski et al., 2017), might possibly also be explained by differences in gazing behavior. In the attentive condition of Kaminski et al. (2017), the human was standing 1 m from the dog. Hence, to look at the human's face, the dogs would have to move their head and/or eyes upwards, which is less likely to have occurred in the inattentive condition, in which the human had her back turned to the dog. Thus, the increased production of the inner brow raiser could be an artifact of variation in gaze behavior between the two conditions.

The same explanation could potentially account for the observed differences in the production of the inner brow raiser reported in the comparative study with dogs and wolves (Kaminski et al., 2019). Dogs have been found to gaze more at humans' faces than wolves (Miklósi et al., 2003; Gácsi et al., 2005); hence the increased frequency of the inner brow raiser shown by the dogs in Kaminski et al. (2019) would be consistent with the dogs looking at the experimenter's face more often than the wolves. A study comparing captive wolves and dogs furthermore indicated that dogs are more alert during resting than wolves (Kortekaas and Kotrschal, 2019), which may also be associated with a higher likelihood of dogs responding to the human experimenter in the study by Kaminski et al. (2019). Moreover, the test conditions differed between species in Kaminski et al. (2019). Whereas the dogs were tested in kennels at an animal shelter, the wolves were tested in their home enclosure at an animal park. However, a person is likely to attract greater attention, and thus gazing, from shelter dogs, which are often relatively deprived of human contact, than from wolves at a wolf park. Besides, the wolves' enclosures were likely larger than the dogs' kennels, which would place the dogs closer to the human observer. This might have caused the dogs to look upwards more than the wolves, potentially leading to more accompanying brow movements. Dogs' tendency to seek human proximity (e.g., Gácsi et al., 2001; Topál et al., 2005; Barrera et al., 2010) could have further increased this effect. These alternative lower-level explanations for the results of the previous studies remain speculative but seem to be consistent with all data now available. Future studies could test this hypothesis further by systematically varying the above-described conditions in both species under otherwise identical testing conditions to examine these suggested associations and further explore the importance of different factors influencing the occurrence of the inner brow raiser.

The fixed order of testing could be considered a potential limitation of the current study; however, we did not expect test order to considerably affect our findings, as a previous study with a similar methodology demonstrated no carry-over effects from previous trials on dogs' facial expressions (Bremhorst et al., 2019), and likewise, no effect of trial number on the dogs' facial expressions was reported in Kaminski et al. (2017). To test for potential order effects, we assessed the relationship between the inner brow raiser and sample order, which was non-significant. Furthermore, neither reward type (the toy condition always preceded the food condition) nor valence (the positive samples always preceded the negative samples) significantly affected the frequency of the inner brow raiser (see **Table 1**). These findings make it unlikely that our results can be explained by testing order.

To conclude, we propose a cognitively lower-level explanation for the differential occurrence of the inner brow raiser in dogs depending on the sociality of the context. Our work emphasizes the importance of considering alternative explanations for what might appear superficially to be functional behavioral expressions.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by the cantonal authority for animal experimentation, the Veterinary Office of the Canton of Bern (Switzerland) (License no. BE62/18 30385) and the College of Science Research Ethics Committee, University of Lincoln (United Kingdom) (UID CoSREC304). Written informed consent was obtained from the owners for the participation of their animals in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

AB, SR, DM, and HW developed the study concept, design, and interpreted the data. AB conducted the experiments and drafted the initial manuscript. LS and AB (both certified DogFACS coders) coded the video samples using DogFACS. All authors reviewed and edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.568935/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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