CURRENT PERSPECTIVES IN COGNITIVE PROCESSING BY DOMESTICATED ANIMALS

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CURRENT PERSPECTIVES IN COGNITIVE PROCESSING BY DOMESTICATED ANIMALS

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EDITORIAL
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Editorial: Current Perspectives in Cognitive Processing by Domesticated Animals

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Editorial on the Research Topic

Current Perspectives in Cognitive Processing by Domesticated Animals

Recently, studies of cognitive processing in domestic animals, especially dogs, seem to have increased exponentially, and research with more typical laboratory animals, such as rats, pigeons, and non-human primates seems to be declining. Funding for behavioral and/or cognitive work with animals has always been challenging, and as costs for animal housing, care, and per diems have increased significantly in the past two decades, researchers have looked to other subject pools that do not require major funding for conducting relevant and important studies that can contribute significantly to our field. Thus, companion animals, notably dogs, have become an important resource for studies of animal cognition, as well as other accessible and less-studied species like goats, horses, and pigs, among others. The Research Topic, entitled "Current Perspectives in Cognitive Processing in Domestic Animals," included 10 papers covering a range of topics and species, with summaries of each paper provided here.

In the initial paper, Csoltova and Mehinagic presented a review and summary of recent research on assessment of dog positive-emotion. They describe a variety of new methodologies, measures, approaches, and techniques looking at the perception, processing, and response assessment in dog positive emotion research. While much past effort has focused on the negative aspects of emotional reactivity and responding by dogs under conditions of duress or fear, these authors provided aspects of positive emotion evaluation of dogs and proposed possible new directions for future research in both short-term and longer-term emotional states assessment in dogs. Finally, the review points out potential limitations and needs in current research methods. In a second paper using dog subjects, Kiss et al., the investigators explored how dogs' attention was affected by their owners attention or inattention to their performance during a fetching task with an unfamiliar person. They were concerned whether the dogs were susceptible to the "audience effect," that is, was their performance affected if they were being watched by their owner or if they were instead ignored. Dogs' performance and behavioral responses were recorded, and these data were subsequently complemented with the dogs' spectral EEG sleep profile which was recorded during a 3-h daytime nap that the dogs took in the laboratory. The results indicated a relationship between the individual dog's susceptibility to the audience effect and the spectral power of REM and non-REM sleep. Both sets of findings provide support for dogs' human-like susceptibility to the audience effect, and how such a trait may be linked to more complex mechanisms like reputation management.

A third paper that presented findings from dogs also provided comparative data from captive born wolves, to look for similarities and differences between the two species on a quantity

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discrimination task. Numerical skills have been examined in a wide range of species to date, from mammals like non-human primates to birds, fish, even salamanders, and evidence for rudimentary to sophisticated numerical competence have been demonstrated across a variety of tasks. In this study, Rivas-Blanco et al. compared the ability of dogs and wolves to recognize either the larger or small of two arrays presented simultaneously as an array of dots on a touchscreen, computer-interfaced system. The apparatus allowed both canid subjects to make their selection on glass panes in front of the screen, using their muzzles, and the pressure-measuring sensors were then activated and linked to a computer which controlled the trials, subjects' data, and activated a remote reward dispenser. Stimulus pairs in the small range included 1–8 dots in an array and combinations of larger numbers (8–32 dots). Arrays were controlled for cumulative surface area, size, and position on the screen. Results indicated that dogs were able to discriminate between two numbers, and their performance was worse as the ratio between the numbers increased, thus conforming to Weber's Law. However, non-numerical variables like dot size did have an impact on performance. In a second study, hand-reared wolves completed the same task, and they, too, were able to distinguish between two quantities of increasing ratios, and performance also both species. It was not possible to determine whether two distinct number processing systems were operating in either species, as have been speculated for other species similarly tested. In both species tested here, they may have used non-numerical cues, when possible, as well as the numerical information, to solve the task. Overall, both studies provide ample evidence that both dogs and wolves can readily distinguish between quantities of varying ratios and magnitudes but will depend upon non-numerical cues if available. These studies also provide insights and suggestions for future research comparing dogs and wolves on quantity judgments and other cognitive phenomena.

In the next paper focusing on dog subjects, Savalli and Mariti present a thoughtful review of current ideas about the role of caregivers and their dogs, using the term "tutor" to represent the human caretaker, either child or adult, and the relationship between the two species. Clearly the potential for a strong bond exists in dogs and humans, as, as the authors explore, Bowlby's Attachment Theory provides an intriguing mélange of theoretical perspectives and possibilities for the emergence of these bonds, and their impact on both the tutor and the dog. They also suggest that Attachment Theory alone is insufficient to account for the range of two-way interactions between dog and tutor, and proposed that Friendship Theory, while typically not applied to non-human animals, might bridge the gap for explaining the depth and range of bonding that occurs between us and our dogs, or that which emerges as a child grows up with a dog companion. Similarly, relationships between conspecifics, as observed in other species like primate, are also discussed, including the early relationships between female dogs and their offspring, and later relationships between adult dogs that live in proximity to one another. Clearly the dog-tutor relationship is a complex one, and Savalli and Mariti remind us that dogs, like humans, possess attachment and caregiving systems, and as such, offer opportunities for new directions in exploring the complexities of these systems in both dogs and humans.

Four of the articles in this Research Topic focus on the cognitive abilities of domesticated species other than dogs. Croney and Boysen describe an innovative set of procedures to train two Panepinto micro pigs and two Yorkshire pigs (*Sus scrofa*) to use a joystick to respond to visual images on a computer screen. Using an adaptation of the SIDE task that has been used with rhesus monkeys, Croney and Boysen found that the pigs showed impressive motor dexterity to acquire this task. In addition, they remind us of critical methodological considerations for the study of cognitive abilities in other species, including visual (location of computer screen) and motor (manipulation of the joystick) adaptations that must be assessed prior to testing.

Trosch et al. also emphasize the importance of procedural modifications in data collection in their work with Welsh ponies, *Equus caballus*. In their study on object permanence in horses, they also made several elegant procedural adjustments to rule out alternative interpretations related to specific behaviors of the subject species (e.g., the Clever Hans effect). Across two experiments, they showed that these ponies exhibited Stage 5a object permanence, that is, retrieval of an object that had been hidden in two or three locations (visible displacement). In addition, the findings of both the Croney and Boysen and Trosch et al. studies highlight the applications of cognitive processing studies to improving animal welfare.

Lansade et al. also studied Welsh ponies but focused on implications of cognitive processing related to specific interactions with humans. In a set of studies on horses' recognition related to humans, Lansade et al. showed that these ponies discriminated familiar and unfamiliar photographs of human faces even when salient features of the faces were altered (e.g., hair length or color, visibility of eyes, facial orientation). Further, they reported some preference for these familiar, but previously unencountered, humans in social tests. These data underscore the impact of the coevolution of humans and horses showing the extraordinary attention to and discrimination of human features by some domesticated species.

Nawroth et al. reported that goats (*Capra hircus*) can use some human pointing cues to identify containers that contain food rewards, in a version of the Object Choice Task (OCT). In this protocol, one of several containers was covertly baited with a reward, and an experimenter provided a pointing gesture to the baited container. Twenty goats were recruited for the study and administered a pre-test to determine whether they would follow a pointing gesture to the baited bucket for six consecutive trials: nine goats reached this criterion. These goats were tested with three different pointing gestures—proximal (sitting between the two buckets, pointing to the baited bucket about 30 cm. from the pointing finger, crossed (sitting between the two buckets, pointing to the baited bucket across the experimenter's body, about 48 cm. from the pointing), and asymmetrical (sitting behind one bucket and pointing to the other bucket at about 90 cm.). These experimental conditions were compared to a control condition in which the experimenter displayed no pointing cue. The goats performed better when the end of the digit was relatively close to the target container (proximal and crossed), compared to the asymmetrical and control conditions. This demonstration adds to a large and growing literature on the capacity of domesticated animals to follow human communicative cues.

In a series of three studies, Kubinyi et al. explored the influence of owners' affective expressions on dogs' (*Canis lupus familiaris*) fetching and looking behavior. In the first study, twelve dogs were asked to fetch either a toy or a bracelet; all dogs displayed a pre-test preference for the toy. Kubinyi et al. asked the owners to look at the toy with disgust and at the bracelet with delight. In test trials, both objects were displayed at a short distance, owners directed the dogs to fetch, without giving any directions as to which objects the dogs should fetch. The dogs fetched the toys that they, themselves, preferred—the owners' emotional displays did not "override" the dogs' preferences. In the second study, the objects were presented on a windowsill, out of reach of 51 dogs. In the Toy condition, the owners expressed delight at the toy, matching the dogs' preferences, and in the Bracelet condition, the owners expressed delight at the bracelet. After both objects were placed on the windowsill, the owners commanded the dogs to fetch, again not directing the dogs to either object. Kubinyi et al. measured the dogs' looking times at the objects, finding that, in the matching condition they looked significantly longer at the toy, and there was a trend toward looking longer at the bracelet in the non-matching condition. In a final experiment, with 11 dogs, they found that the dogs were relatively insensitive to owners' direct gaze, suggesting that it was the owners' emotional displays that influenced the dogs' behavior in Study 2.

In another study of dogs' sensitivity to human emotional expressions, Albuquerque et al. presented 52 dogs with a classic detour task, in which a bowl of food was placed behind a V-shaped barrier at the acute angle. In a pre-test phase, the dogs were given the run of the room for 15 s, and six dogs solved the detour task. The study continued with the 46 dogs who failed to find a route around the barrier. The emotional manipulation involved a brief interaction between the demonstrator and the owner that was either positive, negative, or neutral in emotional tone. After this, the test trials began, during which the demonstrator, staying in affective character, baited the bowl in full view of the dogs, thus demonstrating how to circumvent the barrier. Replicating previous research, Albuquerque et al. found that dogs did learn from observing a knowledgeable demonstrator. Contrary to their expectations, however, they also found no influence of the emotional manipulation on dogs' behavior, and they offer several possible explanations for this to inform future research in this area.

Overall, the Research Topic, "Current Perspectives in Cognitive Processing by Domesticated Animals," provides an exciting overview of a range of recent studies of cognition and behavior in a variety of species. From all studies, new directions for research and insightful new theoretical underpinnings for moving forward in the field of comparative cognition have provided our readership with thoughtful ideas for future research.

AUTHOR CONTRIBUTIONS

KB, DL, and SB wrote this Editorial. All authors contributed to the article and approved the submitted version.

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BRIEF RESEARCH REPORT
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Goats Follow Human Pointing Gestures in an Object Choice Task

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Dogs (*Canis lupus familiaris*) are extremely adept in interpreting human-given cues, such as the pointing gesture. However, the underlying mechanisms on how domestic non-companion species use these cues are not well understood. We investigated the use of human-given pointing gestures by goats (*Capra hircus*) in an object choice task, where an experimenter surreptitiously hid food in one of two buckets. Subjects first had to pass a pre-test where the experimenter indicated the location of the food to the subject by a proximal pointing gesture. Subjects that succeeded in the use of this gesture were transferred to the actual test. In these subsequent test trials, the experimenter indicated the location of the food to the subject by using three different pointing gestures: proximal pointing from a middle position (distance between target and index finger: 30 cm), crossed pointing from the middle position (distance between target and index finger: 40 cm), asymmetric pointing from the position of the non-baited bucket (distance between target and index finger: 90 cm). Goats succeeded in the pointing gestures that presented an element of proximity (proximal and crossed) compared to when the experimenter was further away from the rewarded location (asymmetric). This indicates that goats can generalize their use of the human pointing gesture but might rely on stimulus/local enhancement rather than referential information. In addition, goats did not improve their responses over time, indicating that no learning took place. The results provide a greater understanding of human–animal interactions and social-cognitive abilities of farm animals, which allows for the provision of enhanced management practices and welfare conditions.

Keywords: farm animals, human–animal interaction, livestock, referential information, social cognition

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INTRODUCTION

Via their domestication as a companion animal, dogs are extra-ordinarily adapted to living in an anthropogenic environment and to communicate with humans. Dogs, like children, establish attachment bonds with humans (Rehn et al., 2013), refer to humans when confronted with an unsolvable problem (Miklósi et al., 2003), socially learn from humans in a spatial learning task (Pongrácz et al., 2001), and can use human pointing gestures to gather information about their environment (Kaminski and Nitzschner, 2013).

Increased performance in using a human pointing gesture is one of the most prominent outcomes of domestication and is often tested in a so-called object choice task. Here, an experimenter hides food out of sight of a test subject under one of two or three cups. After baiting the cup, the experimenter indicates the location of the food to the subject by a pointing gesture. In this task, dogs cannot only locate the correct location when the gesture is administered in proximity to the correct location. They can also find food rewards located at a significant distance away from the gesturing experimenter (Hare et al., 1998; Lakatos et al., 2009). Additionally, dogs are also able to use novel, unfamiliar cues in which they have had no previous training or exposure (Soproni et al., 2002; Riedel et al., 2008). These results indicate that dogs understand human pointing as a referential signal and do not solely rely on learning and potential enhancement effects (Kaminski and Nitzschner, 2013).

But dogs are not the only species that are able to use human pointing gestures to locate a reward. A number of non-domestic species have also been found to use a human pointing gesture: gray seals, *Halichoerus grypus* (Shapiro et al., 2003), African fur seals, *Arctocephalus pusillus* (Scheumann and Call, 2004), bottlenose dolphins, *Tursiops truncatus* (Xitco et al., 2001) and jackdaws, *Corvus monedula* (von Bayern and Emery, 2009). Regarding other domestic animals, pigs (*Sus scrofa*), and horses (*Equus caballus*) have also been tested in this paradigm (McKinley and Sambrook, 2000; Proops et al., 2010; Nawroth et al., 2014). While most results for these domestic species are positive (but see Gerencsér et al., 2019), it is complicated to assess the actual mechanisms at work when interpreting animals' use of these gestures. Almost all studies in domestic non-canid species used a standard pointing gesture, administered in a sustained, but sometimes also momentary, manner with the experimenter stretching out it's ipsilateral hand and being positioned in the middle between both locations. This makes it prone to alternative, more simplistic explanations regarding the mechanism at work: the hand of the experimenter is always closer to the correct rather than the incorrect location (effect of stimulus/local enhancement) and ipsilateral pointing might be a gesture that is frequently employed by humans in daily interactions with animals (effects of learning). More complex gestures, such as cross-pointing with the contralateral arm, or configural positions of the experimenter, such as placing the experimenter behind the incorrect location, have rarely been investigated in domestic non-canid animals (but see for pigs: Nawroth et al., 2014).

Goats, a species primarily domesticated for products such as meat and milk rather than companionship, have been shown to interact with humans in similar ways to dogs in common test paradigms. When confronted with an unsolvable problem, they show frequent audience-dependent gazing and gaze alternations toward a human experimenter (Nawroth et al., 2016b; Langbein et al., 2018). Goats also improved their performance in a spatial learning task by observing a human demonstrator prior to the test itself (Nawroth et al., 2016a). They are also able to use human pointing gestures, but not the head orientation of an experimenter, to locate a reward in an object choice task (Kaminski et al., 2005; Nawroth et al., 2015). However, the gestures displayed in both experiments were administered with the ipsilateral hand and while the experimenter was positioned in the middle of both locations. It is thus not clear whether goats (or other domestic non-companion species) can generalize this skill to other pointing gestures and/or whether their performance in this task is simple due to stimulus/local enhancement effects. Given the lack of research on domestic non-companion species regarding their use of human pointing gestures, the presumed underlying mechanisms in these species to use these cues are thus not well understood.

To extend our knowledge on the use of human pointing gestures in domestic non-companion animals, we investigated the use of human-given pointing gestures by goats in an object choice task. We extended the administered repertoire of pointing gestures used in previous experiments on goats to infer whether they generalize between cues and whether they, to some degree, understand their referential nature. Goats were first tested on a proximal pointing gesture (pre-test). Afterwards, they were additionally confronted with a condition that differed in appearance and was displayed at a similar distance to the target (testing for generalization of pointing gesture), and a condition that looked similar to the initial proximal pointing gestures but was administered from an increased distance to the target (testing for comprehension of referentiality). If goats are solely relying on stimulus/local enhancement, we would predict that they would be able to solve the conditions with the proximal distance to the rewarded location, while they would fail to solve the task with an increased distance. Alternatively, if goats would be able to use the referential information from the pointing gesture, we would expect them to solve all three conditions.

ANIMALS, MATERIALS, AND METHODS

Ethics Statement

Animal care and all experimental procedures were in accordance with the ASAB/ABS Guidelines for the Use of Animals in Research (Association for the Study of Animal Behaviour, 2016). The study was approved by the Animal Welfare and Ethical Review Board committee of Queen Mary University of London (Ref. QMULAWERB072016). All measurements were non-invasive, and the experiment lasted no more than 15 min for each individual goat. If the goats had become stressed, the test would have been stopped.

Subjects and Housing

The study was carried out at Buttercups Sanctuary for Goats, United Kingdom[1]. A total of 20 goats, which included 13 neutered male and seven female goats of various breeds and ages, were used (**Table 1**). Goats were fully habituated to human presence and the test arena because of previous research (Baciadonna et al., 2016; Nawroth et al., 2016b). Routine care of the animals was provided by sanctuary employees and volunteers. The goats had *ad libitum* access to hay and were not food restricted before testing. Subjects were tested from 11:00 to 16:00 during August 2016.

Experimental Procedure

The research consisted of two stages: a pre-test session and two test sessions, each administered on separate days. For both,

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[1] http://www.buttercups.org.uk

TABLE 1 | Names, sex, age and breed of the twenty goats that participated.

Name	Sex	Age	Breed	Participation in test
Annie	Female	3	Boer	Yes
Dingle	Male	5	Mix	Yes
Gilbert	Male	11	Pygmy	Yes
Jimmy	Male	8	Pygmy	Yes
Leo	Male	4	Pygmy	Yes
Pooky	Female	4	Pygmy	Yes
Ralph	Male	4	Pygmy	Yes
Vern	Male	6	British Toggenburg Mix	Yes
Sticky	Male	7	Mix	Yes
Archie	Male	10	Pygmy	No, did not reach criterion
Cicero	Male	5	Anglo Nubian	No, did not reach criterion
Hattie	Female	4	British Toggenburg X Pygmy	No, did not reach criterion
Marnie	Female	3	Pygmy	No, did not reach criterion
Rodney	Male	9	Pygmy	No, did not reach criterion
Roland	Male	8	Mix	No, did not reach criterion
Sandy	Female	17	Pygmy	No, did not reach criterion
Heidi	Female	5	British Toggenburg	No, lacked motivation
Nadia	Female	6	British Saanen	No, lacked motivation
Rupert	Male	6	British Toggenburg	No, lacked motivation
Wilfred	Male	5	Anglo Nubian	No, lacked motivation

TABLE 2 | The three pointing gestures plus the control condition that were administered to the goats in the pre-test and test trials.

Condition	Description
Proximal (pre-test and test)	The experimenter dynamically pointed at the bucket containing the food reward until the goat approached either of the two buckets. When the goat approached within approximately 1.5 m of either bucket, the experimenter stopped the dynamic gesture and displayed a sustained pointing gesture toward the rewarded bucket. The baited bucket was positioned approximately 30 cm away from the tip of the experimenter's finger when the arm was fully stretched
Crossed (test)	The same as the proximal gesture (including preceding dynamic pointing) but the experimenter pointed across her body to the bucket with the food reward on the opposite side of her body. The baited bucket was positioned approximately 40 cm away from the tip of the experimenter's finger when the arm was fully stretched
Asymmetric (test)	The same as the proximal gesture (including preceding dynamic pointing) but experimenter sat behind the bucket that did not contain the food reward and pointed across to the bucket that was baited with the food reward. The baited bucket was positioned approximately 90 cm away from the tip of the experimenter's finger when the arm was fully stretched
Control (test)	The experimenter sat motionless with her hands behind her back and was facing the goat

each goat was separated for no longer than 15 min in a large, fenced arena (length: 700 cm, width: 530 cm). The tested subject was always able to maintain olfactory and auditory contact with conspecifics. The main experimenter and an assistant who handled the goats were also present within the arena with the test goat. The experimenter was seated on a small, plastic table at one end of the arena and the assistant was positioned at the opposite end of the arena approximately 350 cm away holding the test subject on a leash at the start point. Two red buckets (height: 25 cm, diameter: 25 cm) were positioned on either side of the experimenter, approximately 200 cm apart, in which a food reward (a piece of uncooked pasta) was placed into one of the buckets before a trial started. The pointing gesture was always directed at the bucket that was baited with the food reward.

Pre-test

In the pre-test, the goats ($N = 20$) were exposed to a proximal pointing gesture (**Table 2**). The location of the food reward was alternated between both sides and was for no more than two consecutive trials on the same side. Before the pre-test began, the test goat was exposed to two training trials. The goat was shown the reward being placed into one of the buckets and was then allowed to retrieve the food, which familiarized the subjects with the buckets. Before each pre-test trial started, the experimenter placed both hands into each bucket simultaneously during baiting so as not to indicate the location of the food reward to the goat. A trial started when the assistant released the goat from the start point. The experimenter pointed at the bucket that contained the food reward at a maximum of five times in a dynamic manner. When the goat approached within approximately 1.5 m of either bucket, the experimenter stopped the dynamic gesture and displayed a sustained pointing gesture toward the rewarded bucket. To accompany the pointing gesture, the experimenter also alternated her head orientation between the subject and the bucket to further reinforce the communicative nature of the cue. Each goat received two training trials and a maximum of 16 trials in the pre-test, all administered on one day. If a goat chose the baited bucket in six consecutive pre-test trials (binomial test, $P = 0.031$), it proceeded to the test.

Test

Procedure for test trials was similar to that of the pre-test trials with the exception that goats ($N = 9$; two females, seven males) were exposed to four different conditions: proximal pointing, crossed pointing, asymmetric pointing and a control condition (**Table 2** and **Figures 1a–d**). In all conditions, excluding the control condition, the experimenter pointed at the bucket that contained the food reward at a maximum of five times in a dynamic manner. When the goat approached within approximately 1.5 m of either bucket, the experimenter stopped the dynamic gesture and displayed a sustained pointing gesture toward the rewarded bucket. To accompany the three pointing gestures, the experimenter also alternated her head orientation between the subject and the bucket. Test trials started three days after the pre-test and were administered over two sessions (one per day) including 16 trials each. Identical to the pre-test, each test session started with two motivation trials where the goat was shown the food reward being placed in either bucket (left–right or right–left). In the test trials, each of the four conditions was

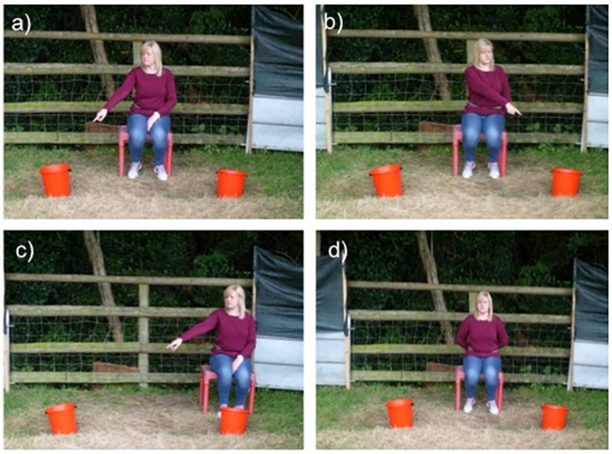

FIGURE 1 | Images of the four test conditions: **(a)** proximal (the whole arm is visibly pointing at the rewarded bucket), **(b)** crossed (the arm is pointing at the rewarded bucket, but only the wrist and hand are clearly visible), **(c)** asymmetric (the whole arm is visibly pointing at the bucket, while the experimenter is positioned behind the non-rewarded bucket), and **(d)** control.

presented to the goat four times pseudo-randomly within the 16 trials of each session and was not presented more than twice in a row. The location of the food reward was also alternated and pseudo-randomly balanced between both sides and was for no more than two consecutive trials on the same side.

Data Coding and Analysis

A digital video camera (Sony HCR-CX 190E Camcorder) was used to record the trials, which was placed on a tripod and positioned behind the fence where the experimenter was seated. We scored which bucket (correct or incorrect) the test subject chose for each trial. Choice was defined as physical contact of the goat with the bucket. If a goat needed more than 60 s to indicate a choice, the trial was scored as "no choice." We also scored if goats approached the index finger of the experimenter before making a choice (from physical contact to 5 cm distance between finger and goat). The latter was done to assess whether goats were only attracted to the hand movement of the experimenter, rather than the pointing direction itself. To assess inter-observer reliability, 50% of the videos were coded by a second coder unfamiliar to the initial hypothesis. Inter-observer reliability for choice analysis (Cohen's $\kappa = 0.972$, $P < 0.0001$) showed a very high level of agreement. Statistical analyses were carried out in R v.3.6 (R Core Team, 2017). The choice behavior of goats in the test trials was treated as a binary variable (choose correct bucket = 1, choose incorrect bucket = 0) and was analyzed with a generalized mixed-effects model fit with binomial family distribution and logit link function (GLMM; glmer function, lme4 library; Pinheiro and Bates, 2000). "Condition" (factor with four levels: proximal, crossed, asymmetric, control) and "Session" (factor with two levels: 1, 2) as well as their interaction were included as fixed factors. The statistical significance of the factors was assessed by comparing the models with and without the factor included. *P*-values were calculated using likelihood ratio tests (LRT) and when a significant effect of "Condition" was detected, we carried out Tukey *post hoc* tests (glht function, multcomp library, Hothorn et al., 2008). Identity of the goats was included as a random factor to control for repeated measurements. To analyze whether the group performance in each condition deviated from random chance level (i.e., 4 out of 8 trials correct) we used one-sample *t*-tests. Goats rarely approached the index finger of the experimenter when one of the three pointing gestures were administered (in 12 out of 216 test trials, excluding the control condition) so we only provide descriptive statistics on this factor. All tests were two-tailed, and the alpha level was set at 0.05 for all statistical tests. An example video, as well as raw data and code can be found in the **Supplementary Material** and here: https://osf.io/vy5md/.

RESULTS

Pre-test

Of the 20 goats that participated in the pre-test, nine goats advanced to the test trials (mean ± SD: 9.33 ± 3.2 sessions). Seven goats completed the 16 pre-test trials but did not reach the criterium and were thus excluded. Four additional goats stopped participating due to a lack of motivation.

Test

Goat performance in locating the correct bucket in the task differed significantly across conditions (GLMM: $n = 288$ trials, 9 goats; $X^2 = 33.143$, $P = 0.001$; **Figure 2**). Neither "Session" nor an interaction between "Condition" and "Session" was found ("Session": $X^2 = 0.774$, $P = 0.37$; interaction: $X^2 = 0.489$, $P = 0.92$). *Post hoc* Tukey tests revealed that the goats chose the correct bucket more often in response to the proximal pointing gesture compared to the asymmetric pointing gesture ($z = 3.293$, $P = 0.006$) and tended to do so compared to the control condition ($z = 2.490$, $P = 0.06$). They also chose the correct bucket more often in response to the crossed pointing gesture in comparison

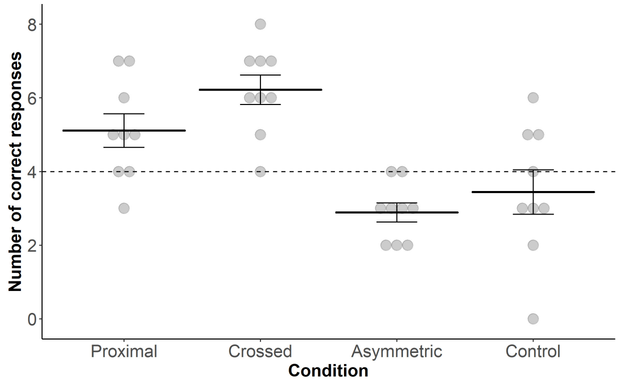

FIGURE 2 | Dot plot including mean performance and standard errors over the four test conditions: proximal, crossed, asymmetric and control. Filled dots represent individual data points. The dashed line represents chance level (i.e., 4 out of 8 trials correct).

to the asymmetric pointing gesture ($z = 4.869$, $P < 0.001$) and the control condition ($z = 4.145$, $P < 0.001$). All other comparisons were not significantly different.

Performance in the conditions "proximal," "crossed," and "asymmetric" differed significantly from chance level (i.e., 50% success rate; proximal, $t_8 = 2.443$, $P = 0.04$; crossed, $t_8 = 5.547$, $P < 0.001$; asymmetric, $t_8 = -4.264$, $P = 0.003$; one-sample t-test); this was not the case for the control condition ($t_8 = -0.921$, $P = 0.384$).

Most goats (6/9) approached the experimenter's hand/finger in one or more test trials before choosing either bucket. However, in total, they only approached the hand/finger in 12 out of 216 test trials (5.55%, excluding the trials of the control condition). In 10 out of these 12 trials, the test subject chose the baited bucket.

DISCUSSION

We investigated the use of different human pointing gestures by goats in an object choice task. Goats succeeded in following the pointing gestures that presented an element of proximity (proximal and crossed) compared to when the experimenter was further away from the rewarded location (asymmetric). This indicates that goats can generalize over pointing gestures but might not be able to use the referential information conveyed in those gestures (Miklósi and Soproni, 2006; Krause et al., 2018).

Goats performed well when confronted with the proximal and the crossed pointing gestures, but not in the asymmetric condition. The first two gestures included a decreased distance between the index finger of the experimenter and the rewarded bucket, compared to the asymmetric condition. This indicates that stimulus/local enhancement and/or positive reinforcement to approach a human hand (or the human itself) might best explain the good performance in the proximal and crossed condition (Krueger et al., 2011; Bensoussan et al., 2016). However, the low direct approaches to the experimenter's finger indicate that goats did not show increased interest to physically interact with the experimenter *per se*.

Goats in our study approached the bucket that was indicated by a human pointing gesture in the asymmetric condition significantly less likely compared to chance level, indicating that they were attracted by the experimenter positioned at the location of the incorrect location. However, we cannot completely rule out that goats might use referential information in this context, as the stimulus/local enhancement by the human positioned behind the incorrect location might have overridden any effect of it. Other test designs, such as an experimenter, placed in the middle, having two cups at an increased distance in front of them (Lakatos et al., 2009) should thus be implemented.

We did not find that goats' performance improved over the two sessions, indicating a lack of learning. They were also not able to locate the hidden reward in the control condition, indicating no inadvertent cueing during the test procedure. Four of the initial 20 goats (20%) lost motivation to participate in the pre-test and were subsequently excluded. This might be due to distractions in the environment or fatigue. While a dropout rate of approximately 20% can be considered the norm in object-choice tasks (Kaminski and Nitzschner, 2013), another seven subjects did not reach the criterion to proceed to the pre-test. The exclusion of these subjects in the test might have skewed group performance toward higher numbers. However, not reaching the criterion does not equal that goats were not able to follow the pointing gesture. In fact, six out of the seven subjects that did not reach the criterion choose the rewarded bucket in nine or more of the 16 administered trials in the pre-test. In the future, it would be interesting to test other populations of goats with different backgrounds regarding their interactions with humans. Goats in our study lived at a sanctuary and experience daily positive interactions (e.g., feeding and grooming) with familiar and unfamiliar humans. Testing goats of different ages, as well as feral or wild goats, will shed light on the origin of domestic goats' ability to use pointing gestures by humans.

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 the Animal Welfare and Ethical Review Board committee of Queen Mary University of London. Written informed consent was obtained from the owners for the participation of their animals in this study. Written informed consent was obtained from the individuals and/or minors' legal guardian/next of kin for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

CN and AM designed the experiment. CN and ZM collected and analyzed the data. All authors wrote the manuscript and approved it for publication.

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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.2020.00915/full#supplementary-material

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Behavioral and Neurophysiological Correlates of Dogs' Individual Sensitivities to Being Observed by Their Owners While Performing a Repetitive Fetching Task

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Ample evidence suggests that dogs possess enhanced skills in reading human visual attention, but it remains to be explored whether they are sensitive to the audience effect in their interactions with humans. The present study aimed to investigate how dogs' behavior is affected by their owners' visual attention while performing a repetitive task (bringing an object back to an unfamiliar experimenter while the owner waited passively). We assumed that if dogs are susceptible to the audience effect, their task persistence and task performance would vary according to their owners' attentiveness. A group of adult pet dogs ($N = 27$) were repeatedly presented with an object retrieval task by the experimenter ($N = 20$ trials) while owners either ignored their dogs (Inattentive Owner condition) or paid attention to their dogs' actions (Attentive Owner condition). Behavioral observations were complemented with the owner's reports of their relationships with their dogs (assessed by means of an owner–pet attachment questionnaire) and dogs' spectral EEG sleep profile (recorded during 3-h-long daytime sleep). Although dogs, independently of their owners' attentional state, were generally willing to comply with the fetching task, they were faster to approach the toy object and gazed significantly longer at their owners when he/she was paying attention. This finding is reminiscent of peer influence observed in humans. Further, characteristics of relationship insecurity (relationship anxiety and avoidance) were associated with dogs' task persistence and performance. Dogs of owners with higher relationship anxiety tended to approach the toy object less frequently, and dogs of owners with higher relationship avoidance and anxiety were more hesitant to approach the toy object. We also found that dogs' individual susceptibilities to the audience effect is related to EEG spectral power of both REM and non-REM sleep as well as in pre-sleep (drowsiness) in a trait-like manner. These results, in line with previous findings, support the notion that dogs have a somewhat human-like susceptibility to the audience effect, a trait which might be linked to more complex mechanisms, such as self-presentation or reputation management, helping the two species to become effective social partners.

Keywords: dog (*Canis familiaris*), dog–human interaction, audience effect, relationship insecurity, sleep EEG

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INTRODUCTION

The ability to monitor the focus of others' visual attention has crucial importance in human social functioning. Since the early experiments of Triplett (1898) a large body of research has been initiated in order to understand and explain the impact of social presence on human behavior. The general finding is that when people think they are being watched, they are less likely to break the social rules (Baillon et al., 2013) and more open for cooperation (Burnham and Hare, 2007). But the phenomenon of the "audience effect" is not restricted to humans; it can also be used to describe social interaction between non-human animals (Coppinger et al., 2017). Ample evidence suggests that the mere presence of conspecifics may affect the behavior of non-human animals in various situations. Social influences can both inhibit and facilitate behavior among group mates as has been reported in wide range of animals, including non-human primates (Visalberghi and Addessi, 2000; Reynaud et al., 2015), other mammals (Sherman, 1977), birds (Evans and Marler, 1994), and fish (Karplus et al., 2006).

Primates, however, respond not just to the mere presence of others, but also to their visual attention. Sensitivity to the visual attention of others is important because it allows group mates to gain information about each other's activities and potential cooperation. Increasing evidence suggests that non-human primates are able to adjust their behavior to others' attention state, and thus, they have at least a basic understanding of "being watched," an important precondition for the emergence of human-like features of the audience effect. For example, olive baboons (*Papio anubis*) adjust their requesting gestures to the state of the eyes (open/closed) of a potential helper (Bourjade et al., 2015). It has also been shown that orangutans (*Pongo pygmaeus*) modify their facial expressions when a recipient is watching them (Waller et al., 2015), and gibbons (*Hylobates* sp.) use their facial expressions differentially depending on the attentional state of others (Scheider et al., 2016).

Although communication usually involves interactions between conspecifics, domestic dogs (*Canis familiaris*) represent a special case among animals as they are not only adept at communicating with conspecifics, but can engage in communication with people (Kaminski and Marshall-Pescini, 2014). Dogs are able to use social signals effectively and purposefully in dog–human interactions, including expressive use of vocalization (Miklósi et al., 2000; Horowitz and Bekoff, 2007), body posture (Quaranta et al., 2007), and visual attention cues (Virányi et al., 2006). Moreover, dogs readily follow human gestural signals (Miklósi and Soproni, 2006) from 6 weeks of age onward (Riedel et al., 2006) and can extract information from vocal intonation cues (Colbert-White et al., 2018). Even though little is known about the socio-cognitive abilities of domesticated species other than dogs, it has been reported that horses (*Equus caballus*) (Maros et al., 2008), domestic cats (*Felis catus*) (Miklósi et al., 2005), goats (*Capra hircus*) (Kaminski et al., 2005), and pigs (*Sus scrofa domestica*) (Nawroth et al., 2014, 2016) are also able to follow certain types of human pointing. These findings highlight the role of domestication as a special evolutionary process that might have caused substantial changes in attention allocation and willingness to cooperate with humans. Dogs also seem to possess those two basic skills that are necessary to respond adequately when being watched: They are sensitive to changes in their partner's visual attention and are able to use the emotional information provided by a human partner. It has been reported, for example, that dogs can take into account the visual access of their human partner in a fetching task (visual perspective-taking; Kaminski et al., 2009) and are less likely to engage in forbidden behavior when the human is looking at them (Schwab and Huber, 2006; Kaminski et al., 2013). Dogs can distinguish between attentive and inattentive human partners and not only recognize human facial expressions (e.g., Siniscalchi et al., 2018), but they also use facial changes in response to changing attention of their human audience (Kaminski et al., 2017). There is also some evidence that they tend to use their owners' affective cues to guide their own behavior toward novel objects (Merola et al., 2012, 2014; Turcsán et al., 2015) in problem-solving tasks. Evidence also suggests that dogs' human-directed behavior (i.e., gazing at the human, approaching a human) is affected not only by social familiarity (Horn et al., 2013), but by the social aspects of the dog–human relationship and the owner's interaction styles toward his/her dog (Topál et al., 1997; Horn et al., 2012). Namely, the specific relationship that a dog has with its human audience influences its attention toward that person.

Most research revolving around the audience effect focuses on the group-level phenomena (i.e., members of certain species react in a certain way to being observed under different conditions). However, as in case of all other socio-cognitive capacities, individual variability can be observed regarding sensitivity to the presence of others. It is, thus, plausible to assume that such variability is related to neurophysiological parameters. Sleep EEG fingerprints are one promising such parameter that have been shown in humans to correlate with individual variability in several domains. For example, attachment patterns (Sloan et al., 2007) and IQ (Ujma et al., 2014, 2015) have been robustly shown to be related to sleep EEG parameters. This means that, while no cause–effect conclusions can be drawn from these correlative studies, there is a significant covariation between the behavioral and the neural measures at the individual level. There are also examples that are potentially relevant to the audience effect phenomena. In addition to tracking the audience engagement (attention level), judging others' emotional reactions is also crucial to one who is observed. Evidence suggests that problems in recognizing and interpreting other people's emotional expressions can lead to poor interpersonal functioning (Shimokawa et al., 2001). Recent studies have revealed an interesting feature of human emotion recognition ability: Emotion recognition and responsiveness to social-affective signals are particularly sensitive to sleep quality (for a review, see Beattie et al., 2014). For example, sleep duration was found to be associated with peer acceptance and social engagement, two components of peer social competence (Vaughn et al., 2015). Sleep disturbance can lead to impaired social interactions (Gilbert et al., 2015) and reduce self-expression in social interactions (Condén et al., 2013) and has the potential to reduce the accuracy of identifying facial expressions of happiness and sadness (Crönlein et al., 2016; Killgore et al., 2017). The effect of sleep deprivation on facial emotion identification was also confirmed by the results of resting state EEG studies. Findings suggest associations among poor emotional processing, left lateralization of alpha power, and increased ratio of the power density (theta/beta ratio) in the frontal area (Zhang et al., 2019). It has also been reported that atypical features of REM sleep physiology (reduced REM sleep gamma EEG activity) predict decreased emotional reactivity (van der Helm et al., 2011).

Personality traits and attachment style are additional important factors in social responsiveness (West and Sheldon-Kellor, 1994), and individual differences in personality factors and attachment have well-documented associations with several sleep parameters. For example, objective measures of sleep quality (e.g., alpha intrusion in non-REM sleep, a marker of hyperarousal during sleep) are associated with attachment anxiety but not with attachment avoidance (Sloan et al., 2007). Studies also showed significant associations between sleep quality and the "big five" personality traits: There is a negative relationship among subjective measures of sleep quality and neuroticism (emotional lability; Calkins et al., 2013), conscientiousness (Williams and Moroz, 2009), and extraversion (Blagrove and Akehurst, 2001).

There is only scarce and circumstantial evidence for the associations between dogs' responsiveness to social-affective signals and sleep parameters. Non-invasive polysomnography studies on dogs showed significant differences in the spectral characteristics of sleep EEG between the active and passive day (Kis et al., 2014). Dogs also display considerable individual variation in sleep macrostructure as measured by sleep efficiency, sleep latency, sleep cycle duration, slow wave sleep, and REM sleep time (Kis et al., 2014), and there are age- and sex-related differences in sigma burst activity during non-REM sleep (Iotchev et al., 2019). However, although the effects of pre-sleep emotions on dogs' subsequent sleep have also been reported in dogs (Kis et al., 2017), very little (if any) is known about the associations between the individual differences in emotion processing, social responsiveness, and sleep.

The current study, therefore, investigated the effects of a human audience on dogs' performance during a repetitive fetching task. More specifically, we aimed to examine the impact of the owner's visual attention on dogs' tendency to bring back an object to an unfamiliar experimenter and to investigate the potential associations among the owner–dog relationship, dogs' task performance and spectral EEG sleep profile. We predicted that a dog's willingness to perform a repetitive fetching task would change in response to the changing attentional state of its owner who is passively watching his/her dog. Namely, we would expect dogs to perform better in a repetitive task when they are being watched than when being ignored by their owners. We would also expect associations between the different aspects of the owners' relationships with their dogs (pet-related anxiety and avoidance) and dogs' sensitivity to their owners' visual attention. Lower scores for pet-related anxiety and avoidance may be associated with better task performance. We also aimed to unravel potential associations between dogs' sleep EEG spectrum and their susceptibility to the audience effect, but due to the exploratory nature of this investigation, we refrained from putting forward any specific hypothesis.

MATERIALS AND METHODS

Ethics Statement

This research was conducted in accordance with the Hungarian regulations on animal experimentation and the guidelines for the use of animals in research described by the Association for the Study Animal Behavior (ASAB). Ethical approvals were obtained from the National Animal Experimentation Ethics Committee for both non-invasive EEG recordings (Ref No. PEI/001/1057-6-2015) and behavioral observations (Ref No. PE/EA/853-2/2016). Owners of the pet dogs participated in the study on a voluntary basis and gave their consent for EEG recordings as well as the behavioral testing of their dogs.

Subjects

Twenty-seven adult pet dogs (18 females and 9 males; mean age: 4.46 years, SD: 2.21) and their owners participated in the test. Dogs were from 22 different breeds and 4 mongrels. Since the experiment was built on the task for dogs to bring back a toy object, only subjects that had been trained to retrieve objects on command were studied.

Experimental Procedures

Behavioral Testing

The experiment took place in a room (5 m × 6 m) at the Institute of Cognitive Neuroscience and Psychology. One chair for the owner and some toys for the dog were placed in the room. The tests were video-recorded from four different angles (using cameras fixed to the walls). Before the trials began, the dogs were led into the room by their owners and allowed to explore the room for 5 min.

The experimental procedure consisted of two phases: (1) *Toy preference test* and (2) *Fetching task*. Phase (1) merely served to choose the toy that motivated the dog, while in phase (2), dogs' behavior was examined in a repetitive fetching task situation, comparing two conditions: when the owner showed attention (Attentive Owner condition) vs. when the owner did not watch (Inattentive Owner condition).

Toy preference test

The experimenter briefly explained the tasks and asked which command the dog was familiar with for bringing back the toy. Then the experimenter familiarized herself with the dog: walked with it and initialized a fetching/rolling game with the dog: called its name and presented three different types of toys. Based on the dog's preference, one toy—the one the dog picked to play with the most—was selected for the experiment, and the rest of the toys were removed from the room.

Fetching task

The owner held the dog on a leash at the starting point, and the experimenter verbally attracted the dogs' attention to the toy object ("Look, here!") while holding the toy visibly in her hand.

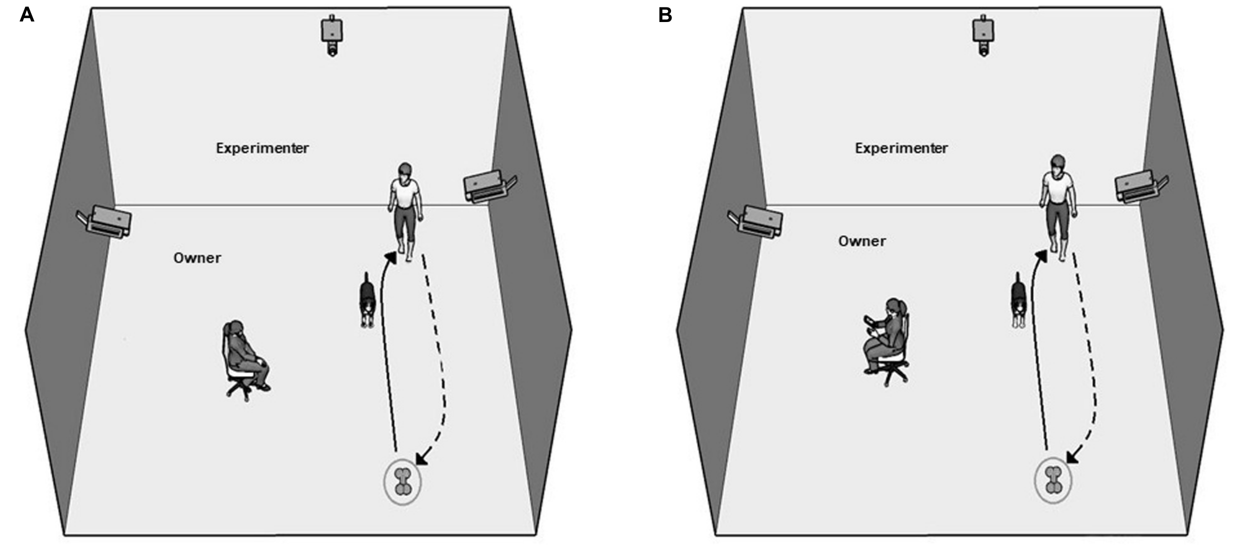

FIGURE 1 | Experimental arrangement in the Attentive **(A)** and Inattentive **(B)** Owner conditions. The path of the experimenter, when she places the toy, is indicated with the arrows.

Then she placed the toy at a predetermined point on the floor (3 m from the starting point) and went back to the starting point, took the leash from the owner, and asked her/him to take a seat.

Attentive Owner (AO) condition (**Figure 1A**): In this condition, the chair faced the field where the dog and the experimenter were. The owner was asked to remain passively in his/her sitting position and to watch the dog silently but attentively. At the moment when the owner sat down and took up his/her position, the experimenter instructed the dog to fetch the toy using a command that the dog was familiar with. The command was repeated once every 5 s until the dog fetched the toy but no more than five times. The dog was praised by the experimenter when it brought back the toy, and the trial was terminated. If, however, the dog did not bring back the toy even after the fifth command, the trial was also terminated. Note, that if the dog refrained from approaching the toy (within 0.5 m) even after the fifth repeated command, the trial was labeled as "Refused."

Inattentive Owner (IO) condition (**Figure 1B**): In this condition, dogs participated in the same procedure as in AO except that the owner's chair was turned around, making the owner face the wall. Furthermore, the owner was instructed to read (a book or mobile phone) and ignore the dog throughout the trial.

The order of IO and AO trials was predetermined and semirandomized so that there were no more than two consecutive trials of the same type. Dogs received a maximum of 20 trials in a single session (10 IO and 10 AO trials in total; N = 21 dogs). However, if a dog performed three consecutive "Refused" trials in both IO and AI each, the *Fetching task* was finished (N = 3 dogs completed only 9, 12, and 13 trials). Moreover, three additional dog–owner pairs gave up further participation in the *Fetching task* before reaching the criterion of 2 × 3 consecutive "Refused" trials; these dogs completed 6, 7, and 14 trials. The whole procedure was video-recorded and analyzed later by two independent observers.

Questionnaire Data Collection

Before the behavioral observations, owners were asked to fill in a questionnaire assessing dog–owner relationship. This 16-item questionnaire was originally developed by Beck and Madresh (2008), and each item was rated on a Likert scale (1–7). The questionnaire includes 16 questions to assess two scales of human–dog relationship insecurity: 8 items for relationship anxiety (Pet-related Anxiety Scale – PANXS) and 8 items for relationship avoidance (Pet-related Avoidance Scale – PAVS). Generally speaking, PANXS relates to the owner's worries about the quality and the future of his/her relationship with the dog, and PAVS relates to expectations about the dog as trustworthy and supportive. These two different aspects of the owners' relationships with their dogs were calculated by summarizing the scores of the variables representing each trait. Cronbach's alpha was used to assess the internal consistency of the factors (α = 0.646 for PANXS and α = 0.644 for PAVS).

Sleep EEG Recordings

Dogs also participated in 3-h-long daytime sleep measurements following the protocol described in Kis et al. (2014). Sleep EEG recordings were performed in a sleep laboratory (2 m × 3 m) either prior to the behavioral observations (on the same day: N = 13 dogs, 10–220 days before behavioral observations: N = 9 dogs) or 2–30 days later (N = 5 dogs). The timing of the recording could vary depending on the preferences of the participating dog owners but was restricted to the period between 12 pm and 6 pm as dogs show the highest propensity to sleep during the afternoon (apart from nighttime; Takahashi et al., 1972). The sleep laboratory was equipped with a mattress on the floor, and owners could decide whether they preferred their dog to sleep on the mattress with them or on the floor next to them. There were no windows in the room in order to ensure constant light conditions, but a table lamp was provided for the owners to read during the measurement. Dogs were allowed a 5–10 min exploration and familiarization and then the owner took place on the mattress and assisted the experimenter throughout the process of fixing surface attached electrodes onto the dog. The dog was rewarded with food during electrode placement if the owner deemed it necessary, social reinforcement (praise, petting) was used in all cases.

The following electrodes were used: Fz and Cz on the anteroposterior midline of the skull as well as F7 and F8 placed bilaterally on the zygomatic arch. A common reference was used for all four electrodes at the Pz position (posterior end of the skull midline). The ground electrode (G) was placed on the left musculus temporalis. Signals were prefiltered, amplified, and digitized at a sampling rate of 1,024 Hz/channel by using the SAM 25?R style MicroMed Headbox (MicroMed Inc, Houston, TX, United States) with hardware passband at 0.5–256 Hz, sampling rate of 512 Hz, anti-aliasing filter with cutoff frequency at 1 kHz, and 12-bit resolution covering a voltage range of ±2 mV as well as second-order software filters at 0.016 Hz (high pass) and 70 Hz (low pass) using System Plus Evolution software (MicroMed Inc., Houston, TX, United States). In addition, electrocardiogram (ECG), respiration, and muscle tone was monitored in order to aid sleep stage identification. Impedances for the EEG electrodes were kept below 20 kΩ .

Behavior Variables

Behavioral data were analyzed by frame-by-frame coding of all experimental recordings (with a 0.2-s resolution, using Solomon Coder (beta 091110, ©2006 by András Péter[1]). The following behavior variables (16) were recorded:

(1) Latency to approach the toy, $\mathrm{LAT}_{\mathrm{Appr/Toy}}$: The time (s) elapsed between the moment when the experimenter instructed the dog to fetch the toy and the moment when the dog arrived at the toy (its paw/muzzle was closer than 50 cm to the toy).
(2) Latency to give the toy over to the experimenter, $\mathrm{LAT}_{\mathrm{Give/Toy/}\mathit{Exp}}$: The time (s) elapsed between the moment when the experimenter instructed the dog to fetch the toy and the moment when the experimenter took the toy in her hand.
(3) Latency to give the toy over to the owner, $\mathrm{LAT}_{\mathrm{Give/Toy/Own}}$: The time (s) elapsed between the moment when the experimenter instructed the dog to fetch the toy and the moment when the dog approached (<0.5 m) the owner with the toy in his mouth.
(4) Gazing at the owner, $\mathrm{WATCH}_{\mathit{Own}}$: Relative duration (t%) of the head orientation toward the owner.
(5) Gazing at the experimenter, $\mathrm{WATCH}_{\mathrm{Exp}}$: Relative duration (t%) of the head orientation toward the experimenter.
(6) Latency of first gaze at the owner, $\mathrm{LAT}_{\mathrm{WatchOwn}}$: The time (s) elapsed between the moment the experimenter instructed the dog to fetch the toy and the moment of the dog's first head orientation toward the owner.
(7) Latency of first gaze at the experimenter, $\mathrm{LAT}_{\mathrm{WatchExp}}$: The time (s) elapsed between the moment when the experimenter instructed the dog to fetch the toy and the moment of the dog's first head orientation toward the experimenter.
(8) Time spent close to the experimenter, $\mathrm{PROX}_{\mathrm{Exp}}$: The percentage of the total time (t%) spent in close proximity (<0.5 m) to the experimenter.
(9) Time spent close to the owner, $\mathrm{PROX}_{\mathit{Own}}$: The percentage of the total time (t%) spent in close proximity (<0.5 m) to the owner.
(10) Time spent close to the toy, $\mathrm{PROX}_{\mathrm{Toy}}$: The percentage of the total time (t%) spent in close proximity (<0.5 m) to the toy object.
(11) Whether the dog approached the toy during the trial (Yes/No), $\mathrm{Binary}_{\mathrm{Appr}}$.
(12) The total number of trials during which the dog approached (<50 cm) the toy, $\mathrm{N}_{\mathrm{Appr}}$.
(13) Whether the dog brought back the toy during the trial (Yes/No), $\mathrm{Binary}_{\mathit{Fetch}/\mathrm{Exp}}$.
(14) The total number of trials during which the dog brought back the toy to the experimenter, $\mathrm{N}_{\mathit{Fetch}/\mathrm{Exp}}$.
(15) Whether the dog tried to involve the owner during the trial (Yes/No), $\mathrm{Binary}_{\mathit{Fetch/Own}}$.
(16) The total number of trials during which the dog tried to involve the owner in the task (i.e., tried to give the toy to the owner), $\mathrm{N}_{\mathit{Fetch/Own}}$.

Two additional variables were used to analyze questionnaire data (Pet-related Avoidance- and Anxiety Scales); see above.

Sleep EEG recordings were visually scored in accordance with standard criteria in 20-s epochs (see Kis et al., 2014, for a more detailed description) identifying the following stages: wakefulness, drowsiness, non-REM, and REM sleep. Artifact rejection was carried out by visual inspection on 4-s epochs using the EEG viewing program Fercio's EEG Plus (©Ferenc Gombos 2009–2017) before further automatic analyses. Average power spectral densities (1–30 Hz) were calculated by a mixed-radix fast Fourier transformation (FFT) algorithm, applied to the 50% overlapping, Hanning-tapered 4-s windows of the EEG signal for the Fz, Cz, F7, and F8 derivations respectively. Relative spectral power values for the different vigilance states (drowsiness, non-REM, and REM) were calculated for each for each frequency bin with 0.25 Hz resolution by dividing the absolute power of the given frequency bin with the total spectral power (on the full 1–30 Hz spectrum).

Statistical Analysis

First we used Wilcoxon matched-pairs signed rank tests to analyze dogs' willingness to participate in the fetching task: (i) the number of trials in which they approached the toy object and (ii) the number of trials in which they brought it back were compared between Attentive and Inattentive Owner conditions.

Then Pearson's correlation analysis was performed to evaluate the strength of association between some of the abovementioned

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[1] http://solomoncoder.com/

behavior variables (latency measures, durations of gazing, and whereabouts of dogs; see variables 1–10 above). After having removed the uninformative (redundant) variables from further analyses, dogs' "Fetching Task" behavior was analyzed with random intercept generalized linear mixed-effect models (GLMM, IBM SPSS 23). The models included a random grouping factor (subject IDs), two fixed factors (Condition – Attentive vs. Inattentive Owner; Numerical order of trials – from 1 up to maximum 20) and covariates (Pet-related Avoidance and Anxiety scales) as well as all combinations of two-way interactions. Non-significant effects were removed from the model in a stepwise manner (backward elimination technique). Statistical tests were two-tailed, and α value was set at 0.05.

In order to assess the relationship between dogs' sensitivity to being watched and sleep parameters, we calculated difference scores between Attentive and Inattentive Owner conditions for all behavioral variables (selected after eliminating redundant variables). These difference scores were then correlated with partial correlations with the relative spectrum using a bin-by-bin analysis on the full (1–30 Hz) spectrum with 0.25 Hz resolution, factoring in the time between sleep and behavioral measurements. In order to address the issue of multiple comparisons, we used the procedure of descriptive data analysis delineating the so-called Rüger's areas (Abt, 1987). Rüger's areas are defined as sets of conventionally significant ($p < 0.05$) results, which are accepted or rejected as significant as a whole instead of individual results of statistical tests. Taking the results of the statistical tests as a matrix, we defined Rüger's areas along the dimension of frequency bins. Starting from the lower frequencies, a Rüger's area is the range of all the neighboring, consecutive frequency bins that contain a significant result surrounded by bins containing non-significant results. After defining these areas of significance, the number of significant results within the area was calculated, and it was investigated whether at least half of these results were significant at least at 1/2 of the conventional $p = 0.05$ significance level (that is, whether they were below 0.025) and at least one third of them were significant at least at 1/3 of the conventional $p = 0.05$ significance level (that is, whether they were below 0.0167). If both of these conditions were fulfilled, the area as a whole was considered significant. With this method, a single significant statistical test with $p < 0.0167$ theoretically counts as a significant Rüger's area; however, we would not have considered single-bin results as an area.

RESULTS

Dogs' Tendency to Participate in Fetching Task

Dogs performed similarly in the Attentive and Inattentive Owner conditions in terms of the number of trials in which they approached the toy object [Wilcoxon signed-rank test, $Z_{(9)} = -0.77$, $p > 0.05$; Median/AO = 10, IQR/AO = 2; Median/IO = 10, IQR/IO = 3]. The majority of subjects approached the toy in every trial (*N* = 17 and 18 dogs in AO and IO conditions, respectively), and each one of the 27 dogs approached the toy at least once in both conditions. Dogs also performed comparably in the two conditions in terms of the number of trials in which they brought back the toy to the experimenter [Wilcoxon signed-rank test, $Z_{(14)} = -1.35$, $p > 0.05$; Median/AO = 7, IQR/AO = 9; Median/IO = 6, IQR/IO = 9], the majority of subjects retrieved the toy at least once in both conditions (*N* = 23 in AO and *N* = 21 in IO).

Reducing the Number of Redundant Behavioral Variables

There were significant correlations between the variables related to the latency to approach the toy and give it over to the experimenter and/or to the owner ($\mathrm{LAT}_{\mathrm{Appr/Toy}}$ – $\mathrm{LAT}_{\mathrm{Give/Toy/Exp}}$, Pearson's $r = 0.352$; $\mathrm{LAT}_{\mathrm{Appr/Toy}}$ – $\mathrm{LAT}_{\mathrm{Give/Toy/Own}}$, $r = 0.765$; $\mathrm{LAT}_{\mathrm{Give/Toy/Own}}$ – $\mathrm{LAT}_{\mathrm{Give/Toy/Exp}}$, $r = 0.392$, $p < 0.01$ for all). Therefore, only one of these (*Latency to approach the toy*) was included in the GLMM analysis. Moreover, since the relative duration of gazing also significantly correlated with dogs' latency of first gaze at the owner and at the experimenter respectively (WATCH_{Own} – $\mathrm{LAT}_{\mathrm{WatchOwn}}$, $r = -0.142$; $\mathrm{WATCH}_{\mathrm{Exp}}$ – $\mathrm{LAT}_{\mathrm{WatchExp}}$, $r = -0.358$, $p < 0.01$ for both), only the relative duration of gazing at the owner and at the experimenter (WATCH_{Own} and $\mathrm{WATCH}_{\mathrm{Exp}}$) were retained for further analysis. Time spent close to the experimenter, owner, and toy also were not included in the GLMM analyses because these variables significantly correlated with each other ($\mathrm{PROX}_{\mathrm{Exp}}$ – PROX_{Own}, $r = -0.270$; PROX_{Own} – $\mathrm{PROX}_{\mathrm{Toy}}$, $r = -0.374$; $\mathrm{PROX}_{\mathrm{Exp}}$ – $\mathrm{PROX}_{\mathrm{Toy}}$ $r = -0.151$; $p < 0.01$ for all), and these variables also significantly correlated with the relative duration of gazing at the owner (WATCH_{Own}). The results of the correlation analyses are summarized in **Supplementary Table S1**.

The Effects of Owners' Attention and Questionnaire Scales on Dogs' Fetching Task Performance

GLMM analysis showed a significant main effect of the *Condition* on dogs' *Latency to approach the toy* [$\mathrm{LAT}_{\mathrm{Appr/Toy}}$, $F_{(1,432)} = 6.927$, $p = 0.009$; the time it took dogs to reach the toy was shorter in the *Attentive Owner* condition; **Figure 2**]. Moreover, the effect of the *Pet-related Avoidance Scale* was marginally significant [$F_{(1,432)} = 3.597$, $p = 0.059$]; dogs of owners with elevated PAVS tended to approach the toy object later, and there was a significant PAVS × PANXS interaction [$F_{(1,432)} = 5.568$, $p = 0.019$; dogs of owners with lower PAVS *and* PANXS tended to approach the toy object sooner]. There were no significant effects of the *Pet-related Anxiety Scale* (PANXS) and *Trial order* as well as there were no other interaction effects ($p > 0.05$ for all).

We found a significant main effect of the *Pet-related Anxiety Scale* (PANXS) on dogs' willingness to approach the toy [$\mathrm{Binary}_{\mathrm{Appr}}$, GLMM; $F_{(1,476)} = 4.462$, $p = 0.035$; dogs of owners with higher relationship anxiety were less willing to approach the toy; **Figure 3**]. The main effects of the *Condition*, *Trial order*, *Pet-related Avoidance Scale* (PAVS) as well as any interaction effects were non-significant ($p > 0.05$).

Regarding the dogs' behavior toward the experimenter, the GLMM analysis failed to show any significant main effects or

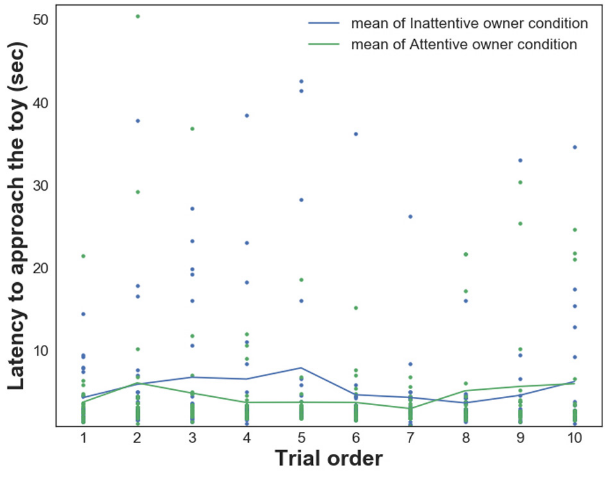

FIGURE 2 | Relationship between dogs' *Latency to approach the toy* and their owners' visual attention in trials 1–10 in each condition.

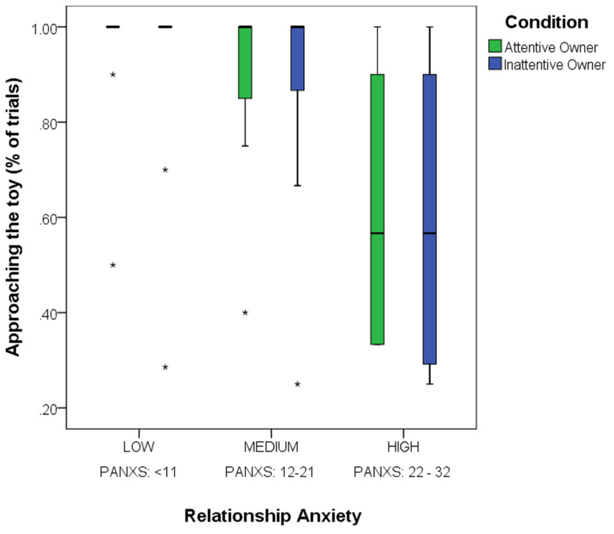

FIGURE 3 | The effect of Pet-related Anxiety (PANXS) on dogs' tendency to approach the toy object ($Binary_{Appr}$) in the Attentive and Inattentive Owner conditions. Dogs are grouped according to their owners' relationship anxiety (medians ± IQT and outliers).

interaction effects on the selected variables (relative duration of gazing toward the experimenter – $WATCH_{Exp}$; tendency to bring back the toy to the experimenter – $Binary_{Fetch/Exp}$; all $p > 0.05$).

Regarding the dogs' behavior toward their owners, however, we found a significant main effect of the *Condition* on dogs' tendency to involve their owners during the trial [$Binary_{Fetch/Own}$, $F_{(1,476)} = 17.747$, $p < 0.001$]. Namely, dogs offered the toy object to the owner more frequently in the Attentive Owner condition (21.9% of the total trials) than in the Inattentive Owner condition (6.3% of the total trials). The main effects of the *Trial order*, *Pet-related Avoidance and Anxiety Scales* as well as the interaction effects were non-significant ($p > 0.05$).

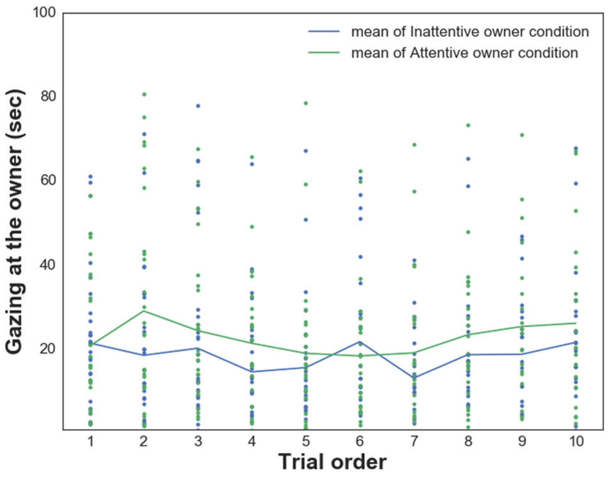

FIGURE 4 | Relationship between dogs' *Gazing at the owner* and their owners' visual attention in trials 1–10 in each condition.

We also found a significant main effect of the *Condition* on dogs' gazing at the owner [$WATCH_{Own}$, $F_{(1,476)} = 10.247$ $p = 0.001$; dogs gazed significantly longer at their owners in the Attentive Owner condition; **Figure 4**]. There were no other main effects (*Trial order*, *PAVS*, *PANXS*) or interaction effects (all $p > 0.05$).

Associations Between Sleep Physiology and Dogs' Behavior in the Fetching Task

Drowsiness

The bin-by-bin analysis revealed that during drowsiness there was a significant positive correlation between $Diff\_N_{Appr}$ (the difference score between the Attentive and Inattentive Owner conditions in dogs' tendency to approach the toy) and EEG spectrum in the 20.0–20.75 Hz and 21.25–22.0 Hz (beta) ranges (**Figure 5**). There was also a significant positive correlation between the difference score of latency to approach the toy ($Diff\_LAT_{Appr/Toy}$) and the relative EEG spectrum power in the 8.5–9.0 Hz (alpha) range. $Diff\_WATCH_{Own}$ (the difference score based on the relative duration of gazing at the owner) was positively correlated with the 6.25–6.75 Hz (delta) as well as with the 11.75–12.0 (alpha) frequency ranges and showed a negative correlation with relative beta activity (in ranges: 16.75–17.75 Hz, 21.75–23.5 Hz, 24.5–30 Hz) during drowsiness (**Figure 6**). As regards questionnaire scores, *Pet-related Avoidance Scale* showed a negative correlation with the relative beta activity in ranges 13.75–16.0 Hz and 19.5–19.75 Hz. *Pet-related Anxiety Scale* was also negatively correlated with the EEG spectrum power in the delta range (1.5–2.5 Hz), and there was a positive relationship between this questionnaire score and the relative beta activity (14.75–15.0 Hz, 15.75–16.0 Hz, 17.5–23.5).

We found no other significant correlations of questionnaire and difference scores with delta, theta, alpha, or beta activities

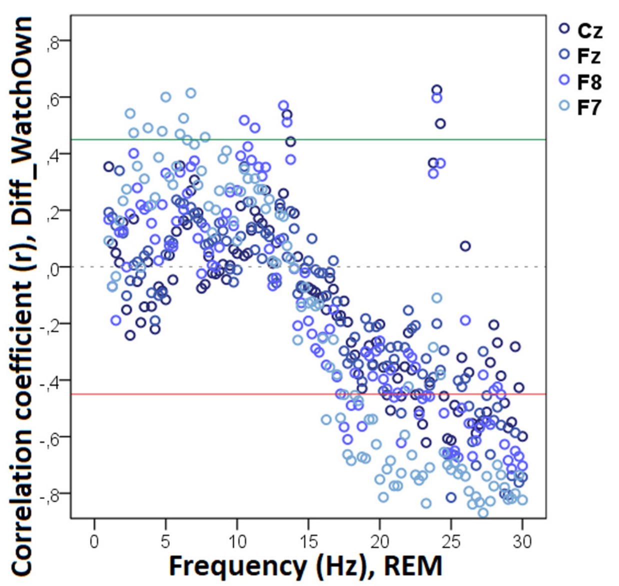

FIGURE 5 | Correlation between the difference in the total number of trials during which the dog approached the toy (Attentive vs. Inattentive Owner condition) and drowsiness EEG power spectrum. Correlation coefficients for the four EEG channels (Fz, F7, F8, Cz) are shown with points above the green line (r = 0.45) and below the red line (r = -0.45) indicating significant ($p < 0.05$) associations for the given frequency bin.

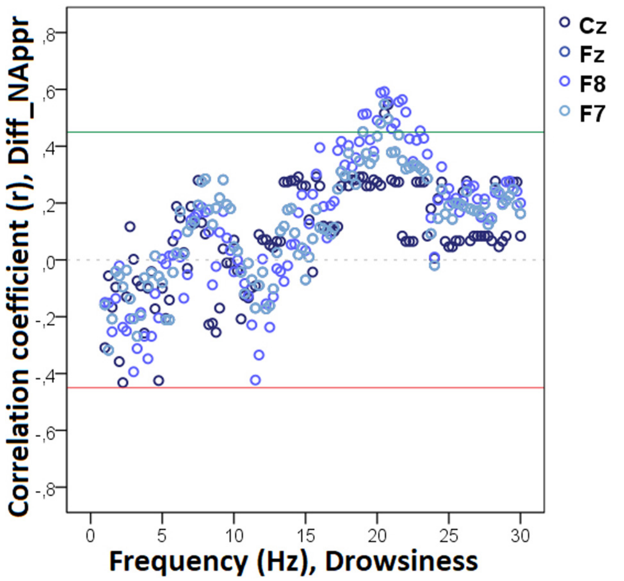

FIGURE 6 | Correlation between the difference in the duration of gazing at the owner (Attentive vs. Inattentive Owner condition) and drowsiness EEG power spectrum. Correlation coefficients for the four EEG channels (Fz, F7, F8, Cz) are shown with points above the green line (r = 0.45) and below the red line (r = −0.45) indicating significant ($p < 0.05$) associations for the given frequency bin.

during drowsiness. See **Table 1** for a summary of the above correlational relationships.

TABLE 1 | Summary of the correlational relationships between the relevant EEG spectrum dimensions and selected behavioral and questionnaire measures during drowsiness.

Behavioral variable	Frequency range (Hz)	EEG channel	Direction of effect
Drowsiness			
Diff_N$_{Appr}$	20.0–20.75 (beta)	F7, F8, Cz, Fz	Positive
	21.25–22.0 (beta)	F8	Positive
Diff_N$_{Fetch/Own}$	–	–	–
Diff_N$_{Fetch/Exp}$	–	–	–
Diff_LAT$_{Appr/Toy}$	8.5–9.0 (alpha)	Cz	Positive
Diff_WATCH$_{Own}$	6.25–6.75 (delta)	Cz, Fz, F7	Positive
	11.75–12.0 (alpha)	Fz, F7	Positive
	16.75–17.75 (beta)	F8	Negative
	21.75–23.5 (beta)	Fz, Cz, F7, F8	Negative
	24.5–30 (beta)	F8, Cz, Fz, F7	Negative
Diff _WATCH$_{Exp}$	–	–	–
Pet-related avoidance	13.75–16.0 (beta)	F7, F8	Negative
	19.5–19.75 (beta)	F8	Negative
Pet-related anxiety	1.5–2.5 (delta)	Cz	Negative
	14.75–15.0	Cz	Positive
	15.75–16.0 (beta)	Fz, Cz, F7	Positive
	17.5–23.5 (beta)	Cz, Fz, F7, F8	Positive

Non-REM Sleep

Our analysis showed that decreased non-REM sleep delta (2.50–4.0 Hz) activity as well as increased alpha (10.0–11.0 Hz) activity were related to higher values in the difference score of the total number of trials during which the dog approached the toy (Diff_N$_{Appr}$; **Figure 7**). The higher differences (AO vs. IO conditions) in the number of fully accomplished trials (Diff_N$_{Fetch/Exp}$) were also related to increased non-REM sleep delta activity (2.5–2.75 Hz). Moreover, the difference score of latency to approach the toy (Diff_LAT$_{Appr/Toy}$) was related to higher theta (6.25–7.0 Hz), alpha (8.0–8.5 Hz), and beta (11. 5–12.5 Hz) activities. There were also significant negative correlations between Diff_WATCH$_{Own}$ and the relative EEG spectrum power in the 15.5–30 Hz (beta) frequency ranges (**Figure 8**). The analysis of the two questionnaire scores (*PAVS*, *PANXS*) indicated that increased theta (4.25–5.0 Hz) activities were related to lower scores of *Pet-related Anxiety Scale*.

We found no other significant correlations of questionnaire- and difference scores with delta, theta, alpha, or beta activities during non-REM sleep. See **Table 2** for a summary of the above correlational relationships.

REM Sleep

Decreased REM sleep delta (1.5–1.75 Hz) activity as well as increased theta (5.25–5.75 Hz) and beta (14.25–14.75 Hz, 15.25–16.0 Hz, 16.25–17.0 Hz) activities were related to higher values in Diff_N$_{Appr}$ (**Figure 9**). The difference in the number of fully accomplished trials (Diff_N$_{Fetch/Exp}$) was negatively correlated with delta activity (1.5–2.0 Hz), whereas this behavioral variable was positively correlated with theta (6.25–6.75 Hz) and beta (12.75–13.0 Hz) activities. Also, in REM sleep, the higher difference score of head orientation toward the owner

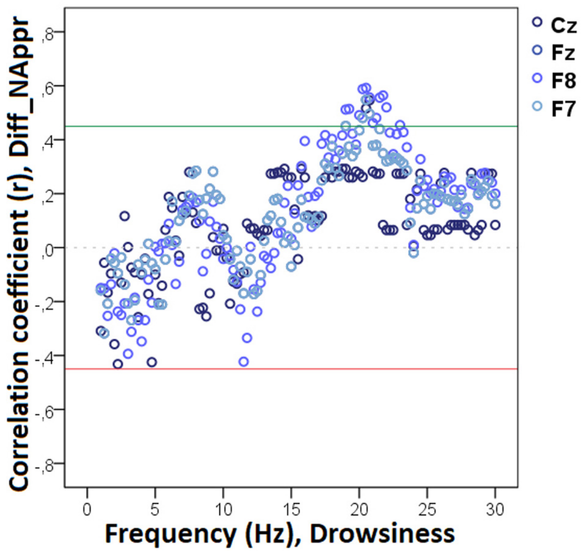

FIGURE 7 | Correlation between the difference in the total number of trials during which the dog approached the toy (Attentive vs. Inattentive Owner condition) and non-REM EEG power spectrum. Correlation coefficients for the four EEG channels (Fz, F7, F8, Cz) are shown with points above the green line ($r = 0.45$) and below the red line ($r = -0.45$) indicating significant ($p < 0.05$) associations for the given frequency bin.

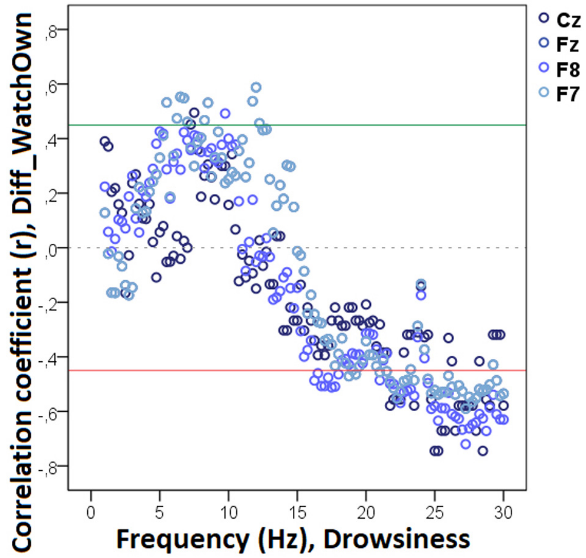

FIGURE 8 | Correlation between the difference in the duration of gazing at the owner (Attentive vs. Inattentive Owner condition) and non-REM EEG power spectrum. Correlation coefficients for the four EEG channels (Fz, F7, F8, Cz) are shown with points above the green line ($r = 0.45$) and below the red line ($r = -0.45$) indicating significant ($p < 0.05$) associations for the given frequency bin.

TABLE 2 | Summary of the correlational relationships between the relevant EEG spectrum dimensions and selected behavioral and questionnaire measures during non-REM sleep.

Behavioral variable	Frequency range (Hz)	EEG channel	Direction of effect
Non-REM			
Diff_N$_{\mathrm{Appr}}$	2.50–4.0 (delta)	Fz	Negative
	10.0–11.0 (alpha)	Fz	Positive
Diff_N$_{Fetch/Own}$	–	–	–
Diff_N$_{Fetch/Exp}$	2.50–2.75 (delta)	F7	Positive
Diff_LAT$_{\mathrm{Appr/Toy}}$	6.25–7.0 (theta)	Fz	Positive
	8.0–8.5 (alpha)	F8	Positive
	11.5–12.50 (beta)	F7, F8	Positive
Diff_WATCH$_{Own}$	15.5–30 (beta)	Fz, F7, F8, Cz	Negative
Diff_WATCH$_{\mathrm{Exp}}$	–	–	–
Pet-related avoidance	–	–	–
Pet-related anxiety	4.25–5.0 (theta)	F7, F8	Negative

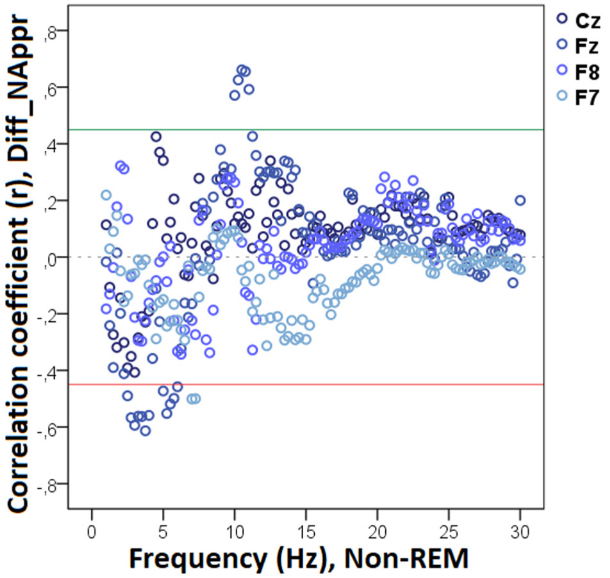

FIGURE 9 | Correlation between the difference in the total number of trials during which the dog approached the toy (Attentive vs. Inattentive Owner condition) and REM EEG power spectrum. Correlation coefficients for the four EEG channels (Fz, F7, F8, Cz) are shown with points above the green line ($r = 0.45$) and below the red line ($r = -0.45$) indicating significant ($p < 0.05$) associations for the given frequency bin.

(Diff_WATCH$_{Own}$) was related to decreased beta activity (ranges: 17.25–18.0 Hz, 18.75–21.75 Hz, 22.25–23.5 Hz, 24.5–30 Hz; **Figure 10**). There was a positive relationship between *Pet-related Avoidance Scale* and EEG spectrum in the 3.0–3.75 Hz (delta) frequency and a negative correlation between *PAVS* and the relative theta activity in the 6.5–6.75 Hz frequency range as well as between PAVS and relative beta activity in the 18.0–18.5 Hz range.

We found no other significant correlations of questionnaire and difference scores with delta, theta, alpha, or beta activities during REM sleep. See **Table 3** for a summary of the above correlational relationships.

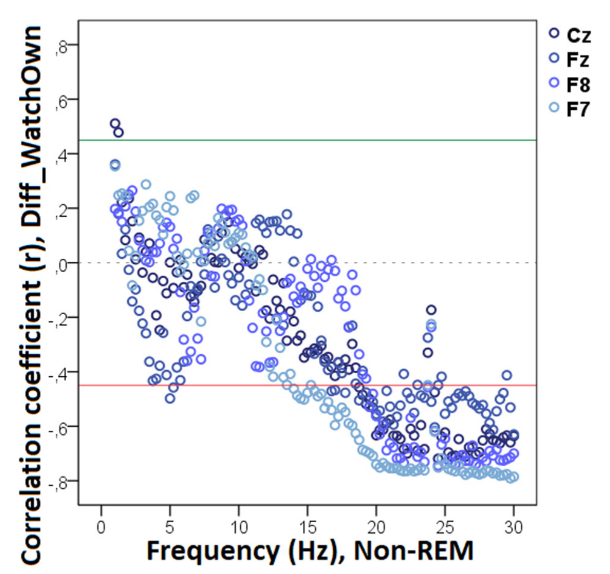

FIGURE 10 | Correlation between the difference in the duration of gazing at the owner (Attentive vs. Inattentive Owner condition) and REM EEG power spectrum. Correlation coefficients for the four EEG channels (Fz, F7, F8, Cz) are shown with points above the green line ($r = 0.45$) and below the red line ($r = -0.45$) indicating significant ($p < 0.05$) associations for the given frequency bin.

TABLE 3 | Summary of the correlational relationships between the relevant EEG spectrum dimensions and selected behavioral and questionnaire measures during REM sleep.

Behavioral variable	Frequency range (Hz)	EEG channel	Direction of effect
REM			
Diff_N$_{\text{Appr}}$	1.5–1.75 (delta)	Cz	Negative
	5.25–5.75 (theta)	F8, Cz	Positive
	14.25–14.75 (beta)	F8	Positive
	15.25–16.0 (beta)	F7	Positive
	16.25–17.0 (beta)	F8	Positive
Diff_N$_{\text{Fetch/Own}}$	–	–	–
Diff_N$_{\text{Fetch/Exp}}$	1.5–2.0 (delta)	Cz	Negative
	6.25–6.75 (theta)	Fz	Positive
	12.75–13.0 (beta)	Cz	Positive
Diff_LAT$_{\text{Appr/Toy}}$	–	–	–
Diff_WATCH$_{\text{Own}}$	17.25–18.0 (beta)	F7, F8	Negative
	18.75–21.75 (beta)	F7, F8, Fz	Negative
	22.25–23.5 (beta)	F7, Cz	Negative
	24.5–30 (beta)	Fz, F7, F8, Cz	Negative
Diff_WATCH$_{\text{Exp}}$	–	–	–
Pet-related avoidance	3.0–3.75 (delta)	Fz, Cz	Positive
	6.5–6.75 (theta)	F7	Negative
	18.0–18.5 (beta)	F8	Negative
Pet-related anxiety	–	–	–

DISCUSSION

The aim of the current study was to assess the potential effect of human visual attention on dogs' performance in a repetitive fetching task. Previous studies have shown that dogs are not only sensitive to the attentional states of humans (e.g., Virányi et al., 2004; Schwab and Huber, 2006; Kaminski et al., 2013; Brubaker et al., 2019), but have a strong propensity to follow instructions and often develop "ready-to-obey" attitudes toward humans (Topál et al., 2006, 2009; Sümegi et al., 2014). Based on these findings, we hypothesized that dogs might be susceptible to the audience effect. More specifically, we expected that dogs' task persistence and task performance would vary according to their owners' attentiveness.

Contrary to our expectations, we found that, independently of their owners' attentional state, dogs were generally willing to follow the experimenter's instructions and to comply with the fetching task. Dogs' comparable task persistence in the Attentive and Inattentive Owner conditions is supported by the analysis of the number of trials in which they approached the toy and brought it back to the experimenter. However, a more detailed behavior analysis revealed that dogs show a somewhat human-like susceptibility to peer pressure. The effect of owners' attention manifested itself through dogs' toy- and owner-related behaviors. They were faster to approach the toy object in the presence of an attentive Owner, gazed significantly longer at their owners, and were more willing to offer the toy to their owners when she/he was paying attention. This finding fits previous observations that dogs are sensitive to the direction of human visual attention when they initiate interaction with humans (see, e.g., Gácsi et al., 2004). More importantly, the observed context-dependent changes in dogs' behavior are reminiscent of effects of peer influence observed in humans (for a review, see Guerin, 1986) and generally support Zajonc's theory of social facilitation (cf. drive theory; Zajonc, 1965). That is, we may assume that like in humans, the attentive (though passive) presence of others increases subjects' arousal, which in turn has the potential to promote social engagement and to facilitate task-related behaviors in dogs. We should note that social facilitation (i.e., the effects of mere presence of a conspecific) has been shown in many different species including non-human primates (Ferrari et al., 2005; Dindo and de Waal, 2007; Reynaud et al., 2015), other mammals (Sherman, 1977), birds (Evans and Marler, 1994), and even fish (Karplus et al., 2006).

Another interesting thing about dogs' behavior in the fetching task is the effect of the owner–dog relationship. Our study provides evidence that the owner's self-assessment of his/her relationship with his/her dog may predict some aspects of dogs' task persistence and performance. Namely, dogs of owners with higher relationship anxiety tended to approach the toy object less frequently, and dogs of owners with higher relationship avoidance and anxiety were more hesitant to approach the toy object. This finding is in line with other observations on the effects of dog–human interaction style on dogs' task performance (Horn et al., 2012; Kis et al., 2012) and may suggest the existence of complex associations between the audience effect in dogs and characteristics of the dog–human caregiver relationship. Note, however, that this was not a direct measure of the dogs' attachment style, and thus, it remains to be investigated which factors really determine the relationship. It seems reasonable to assume that not only relationship insecurity but also other characteristics of the pet–owner relationship as well as the dog's personality, contribute to the behavioral effects of being watched by human caregiver. It would be interesting to examine in future studies how the dog's attachment style is related to the pattern of behavior shown during the observation.

Note, that there were some unusual aspects of the object-retrieval task that the dogs were faced with in our study. First, the experimenter placed the target object on the floor while owners usually throw the ball in such play situations. Most dogs love to chase any thrown object because a moving object helps trigger a dog's prey drive and, thus, raises the arousal level and contributes to the rewarding value of the game (Rooney et al., 2000). Second, everyday object-retrieval games usually require attentional engagement on the owner's part as well as some kind of interactivity by the owner. It is reasonable to assume that, similarly to human children (Meltzoff and Decety, 2003), not only the object-directed activity (retrieval), but the interaction with the owner *per se* is socially rewarding for dogs. In our situation, however, the owner was not responsive (neither encouraged nor praised the dog) even if he/she was watching the interaction.

Analyzing the relationship between dogs' sleep EEG spectrum and fetching task behavior is a pioneering approach to investigate the neuro-cognitive link between dogs' personality traits and their susceptibility to the audience effect. Results show several correlations between difference scores (i.e., changes in dogs' behavior in response to changes in owners' visual attention) and their baseline brain activity. Thus, it appears that a dog's individual susceptibility to the audience effect is a trait-like characteristic reflected in the EEG spectral power of both REM and non-REM sleep as well as in pre-sleep (drowsiness). The bin-by-bin analysis revealed generally consistent significant correlations across all sleep stages in case of two types of behaviors. The first one refers to the change in dogs' task performances, that is, the differences between Attentive and Inattentive Owner conditions in dogs' willingness to do what the experimenter commanded (to approach the toy object, $Diff\_N_{\mathrm{Appr}}$). The second one, however, refers to the change in dogs' tendency to look at their owners ($Diff\_Watch_{Own}$), which can be interpreted as changes in dogs' propensity to initialize interaction with their owners.

Regarding the relationship between dogs' task performances and sleep EEG spectrum, we found that the change in dogs' tendencies to follow the experimenter's instructions was positively correlated with the relative EEG spectrum at the higher frequencies: in the alpha range during non-REM as well as in the beta range during REM and drowsiness. Moreover, the difference score for dogs' tendencies to approach the toy was positively correlated with REM theta, and negatively correlated with low frequency delta during REM and non-REM. The bin-by-bin analysis also revealed a consistent relative beta activity increase in correlation with the differences between Attentive and Inattentive Owner conditions in dogs' tendency to gaze toward their owners in all sleep stages. That is, dogs characterized by higher relative beta power during sleep displayed less flexibility in adjusting their gazing behavior to their owners' attentional state. It should also be noted that some aspects of the human–dog relationship insecurity also were reflected in the spectral characteristics of dogs' sleep EEG. Both Pet-related Anxiety and Avoidance Scales had a robust association with the beta band, but in opposite directions: higher scores of anxiety and lower scores of avoidance scales were related to increased beta activity in drowsiness.

Based on evidence from human studies, we may assume that the increased high-frequency (mostly beta) EEG activity in dogs that tended to show a greater change in following the experimenter's instructions and in gazing toward their owners can be interpreted as a sign of poorer sleep quality. For example higher beta power in non-REM is frequently observed in insomnia patients (Buysse et al., 2008; Marzano et al., 2008; Spiegelhalder et al., 2012), suggesting increased cortical activation resulting from nocturnal emotional and physiological hyperactivation (Spiegelhalder et al., 2011, 2012). The finding that increased alpha EEG activity in dogs is associated with reduced susceptibility to the audience effect (i.e., smaller changes in task performance between Inattentive and Attentive Owner conditions) also parallels results of human studies. That is, a reduced alpha power band is related to more efficient emotion regulation in humans (a higher resistance to immediate emotional impact of the situation; Dennis and Solomon, 2010). Moreover, theta activity during REM sleep, which positively correlated with the difference score for dogs' tendencies to approach the toy, has been reported to be involved especially in consolidation of fear (Popa et al., 2010) and emotional (Nishida et al., 2009) memories in humans. Finally, dogs that showed a smaller response to their owners attention in their tendency to approach the toy had higher delta EEG activity, which, in a way, parallels the human finding that higher delta power in non-REM (stage 4) has been reported in antisocial patients (male subjects with borderline personality disorder; Lindberg et al., 2003).

CONCLUSION

In sum, these results show that dogs accomplish the prerequisites of a human-like sensitivity to being watched, a capacity which might be linked to more complex mechanisms, such as self-presentation or reputation management, helping the two species to become effective social partners. Dogs in the present experiment, despite comparable task persistence in the Attentive and Inattentive Owner conditions, showed several behavioral differences that reflected the effect of owners' visual attention. Their behavior was further related to trait-like parameters, such as the owner–dog relationship and dogs' brain activity during sleep.

Susceptibility to the audience effect is one of the basic "building blocks" of social-emotional capabilities that makes human social cognition unique. It has been previously shown that functionally human-analog social behaviors emerged in dogs, including their sensitivity to the visual attention of others. Even so, any parallels to the underlying mechanisms of the audience effect in humans is still unclear. More research is needed to explore how the relationship with the owner mediates this behavior and what other factors have impact on dogs' social sensitivity manifesting in the increased motivation to conform to the human expectations.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

The animal study was reviewed and approved by National Animal Experimentation Ethics Committee, Hungary. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

OK, AK, and JT designed the study and interpreted the data. OK and KS prepared the study material and data acquisition. KS entered the data and prepared it for statistical analyses. OK, KS, and AK analyzed the data. JT obtained funding. OK wrote the first draft of the manuscript. JT and AK critically revised the manuscript for important intellectual content. All authors gave final approval of the manuscript version to be published and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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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.2020.01461/full#supplementary-material

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REVIEW
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Where Do We Stand in the Domestic Dog (*Canis familiaris*) Positive-Emotion Assessment: A State-of-the-Art Review and Future Directions

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Although there have been a growing number of studies focusing on dog welfare, the research field concerning dog positive-emotion assessment remains mostly unexplored. This paper aims to provide a state-of-the-art review and summary of the scattered and disperse research on dog positive-emotion assessment. The review notably details the current advancement in dog positive-emotion research, what approaches, measures, methods, and techniques have been implemented so far in emotion perception, processing, and response assessment. Moreover, we propose possible future research directions for short-term emotion as well as longer-term emotional states assessment in dogs. The review ends by identifying and addressing some methodological limitations and by pointing out further methodological research needs.

Keywords: behavior, dog, multiple measurement, physiology, positive-emotion

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INTRODUCTION

There has been a growing interest in animal emotion research in recent years. However, positive-emotion has received much less attention than negative emotion thus far. Understanding how an animal perceives, processes, and expresses positive-emotion is crucial not only from a theoretical point of view to improve our knowledge about animal emotion, but also from a practical point of view to improve the animal's life. Concepts such as satisfaction with life, well-being, and welfare refer to more than a mere absence of negative emotions linked to stress and suffering (Mench, 1998; Boissy et al., 2007; Mellor and Beausoleil, 2015; Lawrence et al., 2019); therefore, it is imperative to be able to objectively assess animals perception and processing of, and responses to, positive-emotions.

Specifically, this review focuses on positive-emotion perception, processing, and response assessment in dogs. The review starts with a brief overview of emotion, including its definition, functions of emotion, selected interdisciplinary approaches in the study of emotion, elements associated with and affecting emotion processing, and responses. It is not our intention to dive deeply into the wide and complex field of animal emotion, given the existence of rather extensive literature on the topic (e.g., Harding et al., 2004; Paul et al., 2005, 2020; Burgdorf and Panksepp, 2006; Boissy et al., 2007; Mendl et al., 2009, 2010; de Vere and Kuczaj, 2016; Massen et al., 2019; Kremer et al., 2020). Rather, we emphasize several important key aspects in the study of emotion. Next, we discuss positive assessment in dogs, including the definition of terms such as happiness and pleasure. Thereafter, we continue reviewing measures, approaches, methods, and techniques that have been implemented so far to identify positive-emotion perception, processing, and responses in dogs. Next, we propose possible future directions for research both in short-term emotional responses, as well as for longer-term emotional states assessment in dogs. The review ends by summarizing the main findings, identifying major methodological limitations, and suggesting possible solutions.

A BRIEF OVERVIEW OF EMOTION

Even though there is ample literature on emotion ranging from psychology and neuroscience to animal welfare science, little agreement has been achieved on the concept of emotion. Conceptualization issues have been prevalent over the years and there has been a lot of debate about the definition of emotion. The ability to gain a better understanding of emotion and its complexity is complicated by several different factors. Major debates and disagreements have occurred, regarding the various components that make up emotions, how many emotions exist, the underlying structure of emotions, whether emotions require conscious experience, and how they should be measured (Daroff and Aminoff(eds), 2014; de Vere and Kuczaj, 2016). Furthermore, there are often discrepancies in how the authors define and use the terms across a given manuscript (de Vere and Kuczaj, 2016).

Although a widely accepted definition is missing, emotions are often described as relatively intense, rapid, affective responses to an external stimulus, causing a specific physiological change (Dantzer, 2002; Boissy et al., 2007).

One of the crucial roles of emotion from an evolutionary perspective is to facilitate behavioral and physiological adaptation to a changing environment. The essential survival function of emotions is to seek out rewards and resources while avoiding harm and punishment. The reward is associated with experiencing positive-emotion, while the consequence of reward omission or punishment is a negative emotional experience (Rolls, 2000, 2005).

Several theories have been proposed to explain emotion and emotion processing, both in humans and animals. Among them, is the discrete emotion theory, inspired by Darwin's ideas on the existence of primary emotions reflected in a universal facial expression (Darwin, 1872; Tomkins, 1962; Ekman et al., 1987; Izard, 1994, 2007; Ekman and Cordaro, 2011) and affective neuroscience, which assumes a central role of specific hard-wired neural brain system responses in emotion processing (Berridge, 1996; LeDoux, 1998, 2000, 2012; Panksepp, 2004, 2005, 2011; Burgdorf and Panksepp, 2006; Damasio, 2011).

On the other hand, dimensional approaches, such as the theory of constructed emotion, consider emotions not as universal signals but as potential combinations of external and internal sensations evolved through various distributed brain circuits, which create subjective emotional experiences and perceptions (Barrett, 2006, 2017; Barrett and Wager, 2006). The theory assumes the universal existence of a fundamental conscious neurophysiological affective state called core affect consisting of two dimensions, vertical degree of activation (arousal) and horizontal degree of pleasure (valence) (Russell and Barrett, 1999; Russell, 2003; Barrett, 2006; Duncan and Barrett, 2007).

To bring the discrete and dimensional approaches together, Mendl et al. (2010) have proposed an overarching integrative and functional psychobiological approach for the study of animal emotion. This framework offers a structure for different discrete emotions integration and suggests causal bidirectional interaction between short-term discrete emotions and longer-term mood states. It emphasizes the strong influence of emotional responses to environmental situational factors on an individual's emotional mood and related behavioral, physiological, and cognitive changes. The integrative functional framework also proposes how to measure and predict the impact of emotion-induced cognitive biases on mood states and how these mood states, in turn, impact the stimulus appraisal and decision-making processes (Mendl et al., 2010).

Apart from taking into consideration the mood state when studying animal emotion, here we would like to stress the possible importance of temperament traits in animal emotion assessment studies. Temperament has been considered as a consistent and long-lasting disposition to qualitatively affect both the mood state and the susceptibility to emotional stimuli, speed, and strength of emotion responses (Allport, 1961). Temperament has been defined by certain researchers as a biogenetically determined, relatively stable emotional predisposition to process and express emotions—one that serves as a foundation for personality[1] (Goldsmith et al., 1987). Given that, it is plausible to assume a significant role of certain temperament traits in animal emotion perception, processing, and responses (Boissy, 1995; Boissy et al., 2007; Coleman, 2020; Kremer et al., 2020).

For a long time, it was believed that emotion is independent of cognition (Zajonc, 1980). However, recent neurobiology research has offered proof about the interconnected relationship between emotion and cognition (Okon-Singer et al., 2015).

Besides, research on animals provides further evidence for interactions between emotion and cognitive processes such as learning, memory, attention, judgment, decision making, and social cognition (Harding et al., 2004; Paul et al., 2005; Boissy et al., 2007; Mendl et al., 2009, 2010; Burman et al., 2011; Burman and Mendl, 2018; Hintze et al., 2018; Massen et al., 2019). Hence, examining cognitive processes may prove particularly valuable when studying dogs' positive-emotion processing and responses.

It has been suggested that emotion contributes to cognitive processing, while cognition can play a role in the regulation of emotion (Izard et al., 1984, 2008; Harding et al., 2004; Mendl et al., 2009). For instance, a cognitive appraisal is an assessment that is made about the relevance of a stimulus to oneself at a particular point in time (Lazarus, 1966). The appraisal needs to

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[1] Even though *temperament* and *personality* are often used interchangeably or are not clearly distinguished in animal studies, we adopt the view from human psychology that *personality* is considered a broader concept encompassing individual characteristics that represent a unique consistent pattern of feeling, thinking, and behaving (Cervone and Pervin, 2015).

be made to assign emotional value to stimuli by making use of available information, to determine the appropriate response (e.g., to fear, flee, or feel pleasure). How the animal appraises the information is going to affect the valence and arousal of the emotional response (Paul et al., 2005). However, emotional factors may interfere with correct information processing and create so-called cognitive biases. Cognitive bias is a pattern of a systematic error in cognitive processing by creating a subjective representation of reality that differs from an objective input (Haselton et al., 2015). It is influenced by the emotional state and directly impacts attention, judgment, and decision making. Therefore, cognitive bias can be a useful indicator of emotion in animals (Harding et al., 2004; Mendl et al., 2009, 2010; Bateson et al., 2011; Roelofs et al., 2016; Burman and Mendl, 2018; Clegg, 2018).

To sum up, emotions are short-term reactive responses to emotion-eliciting stimuli (potentially rewarding or punishing) accompanied by physiological changes in the body (Dantzer, 2002; Rolls, 2005; Boissy et al., 2007). They have biological and cognitive foundations. Emotions consist of either positive or negative valence and arousal, ranging from low to high (Russell and Barrett, 1999; Mendl et al., 2010). From a temporal perspective, emotions are closely associated with longer-term mood states and long-lasting, relatively stable temperament traits. Mood, temperament, and cognition seem to play significant roles in emotion processing and responses (Goldsmith and Campos, 1982; Gross(ed.), 2007; Mendl et al., 2009, 2010).

POSITIVE-EMOTION ASSESSMENT IN DOGS

Assessment of positive-emotions in dogs has received only limited attention thus far. Research studies have been focused mainly on negative emotion assessment (e.g., stress, fear, and anxiety) (Dreschel and Granger, 2005; Bergamasco et al., 2010; Travain et al., 2015; Csoltova et al., 2017). One of the possible reasons for this bias is that indicators of negative emotions are much more intense and therefore more easily observed and studied. Positive-emotional states associated with an animal's well-being are usually much more subtle, often less expressive, and often difficult to reliably assess and distinguish from negative emotional states (Boissy et al., 2007). Even though dog well-being and welfare[2] topics have received increased attention in recent years, most of the studies have focused on indicators of compromised dogs' welfare (e.g., Beerda et al., 2000; Rooney et al., 2007; Mariti et al., 2015) or indicators related to the improvement of dogs' already compromised welfare (Hennessy et al., 1998, 2006; Coppola et al., 2006; Bergamasco et al., 2010; Shiverdecker et al., 2013; Csoltova et al., 2017).

Understanding emotions, particularly positive-emotions, is crucial for dogs' well-being. Therefore, there is a huge need for studies focused on the positive well-being and welfare of dogs. Concepts of positive well-being, welfare, and quality of life are closely linked to positive-emotions associated with concepts such as happiness and pleasure (Duncan, 2005; Boissy et al., 2007; Yeates and Main, 2008; Lawrence et al., 2019).

Happiness can be defined as an emotional state that is characterized as a longer-lasting, steady, persistent, and yet less intense positive-emotional experience (Boissy et al., 2007). Animal happiness might include everyday experiences of pleasure, opportunities to interact with their environment, conspecifics, caretakers, and having the freedom to achieve one's own goals (Yeates and Main, 2008).

To the best of our knowledge, pleasure has been the most thoroughly researched positive-emotion so far (e.g., Cabanac, 1971, 1979; Panksepp, 1982; Berridge, 1996; Berridge and Kringelbach, 2008, 2011). Pleasure, although rather a complex phenomenon, is usually associated with subjective hedonic experience (Berridge and Kringelbach, 2011). Pleasure is a passive experience, evoked by an anticipated or received reward, which affects learning, approach behavior, and decision making, as well as possibly contributing to a longer-lasting state of happiness (Schultz, 2015). Pleasure is intertwined with reward-related processes such as *wanting*, *liking*, and *learning* (Robinson and Berridge, 1993; Berridge and Kringelbach, 2008; Berridge et al., 2009). These motivational, emotional, and cognitive processes alternate and co-appear at any time during the pleasure cycle and can be both conscious and unconscious (Berridge, 1996; Berridge and Robinson, 2003; Finlayson et al., 2007; Berridge and Kringelbach, 2008; Berridge et al., 2009). The pleasure cycle (Sherrington, 1907; Craig, 1917; Robinson and Berridge, 1993; Berridge and Kringelbach, 2011) consists of the following time phases (**Figure 1**):

1. The appetitive phase is characterized by *wanting*, motivational processes of incentive salience, desire to obtain the reward (Berridge, 1996; Berridge and Robinson, 1998; Berridge et al., 2009; Kringelbach and Berridge, 2009). *Wanting* is mainly triggered by innate unconditioned or classically conditioned stimuli (Robinson and Berridge, 1993; Berridge et al., 2009). Dopamine seems to be a reward predictor, reflecting *wanting* (Berridge and Robinson, 1998; Wise, 2004; Robinson et al., 2005; Arias-Carrión and Pöppel, 2007; Berridge, 2007; Newquist and Gardner, 2015). This phase is characterized by increased activity, motivation, approach behavior, and associative learning (e.g., remembering food-associated stimuli) (Craig, 1917; Berridge, 1996; Berridge et al., 2009; Schultz, 2015).
2. The consummatory phase is characterized by *liking*. During this stage, the subject experiences sensory pleasure (Berridge, 1996; Berridge and Kringelbach, 2008; Berridge et al., 2009). Opioids, endocannabinoid, and orexin seem to mediate the hedonic *liking* responses to food reward (Peciña and Berridge, 2005; Smith and Berridge, 2005;

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[2] For the purposes of this paper, *well-being* is defined as the animal's complex subjective internal state affected by the animal's perception, cognition, emotion, motivation, and the manifestation of its mental and somatic perception and interpretation of the internal and external stimuli (Clark et al., 1997). The term *welfare* is considered broader, encompassing the overall state of animal's health and physical, social, and mental well-being (adapted from Halverson, 2001). The exception is when we are discussing the work of others who use a different convention.

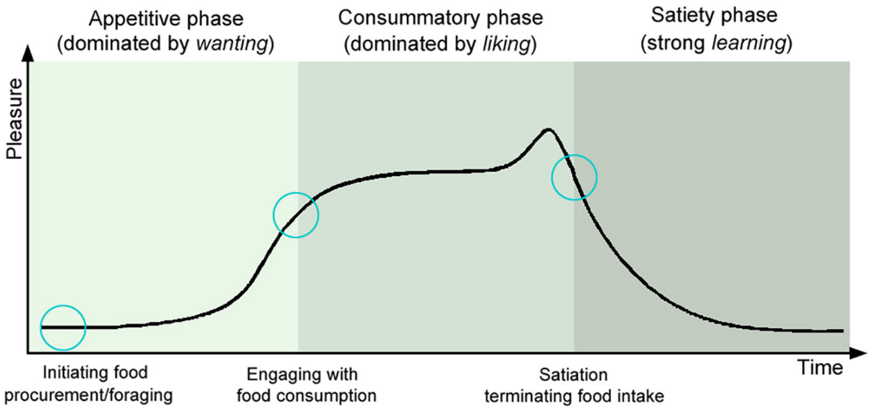

FIGURE 1 | Pleasure cycle phases (adapted from Berridge and Kringelbach, 2011; Rømer Thomsen et al., 2015). Pleasures associated with different social and non-social rewards, follow a cyclical pattern, represented by appetitive, consummatory, and satiety phases (Sherrington, 1907; Craig, 1917). Rewards play a crucial role in initiating, sustaining, and switching between the phases and consist of processes supported by multiple brain networks, each with a specific function in the processing of *wanting*, *liking*, and *learning* elements of the reward (Berridge, 1996; Berridge and Kringelbach, 2013).

Mahler et al., 2007; Ho and Berridge, 2013; Castro and Berridge, 2014).

3. The satiety phase is characterized by strong *learning* about reward predictions based on previous experiences (although learning happens at any phase during the reward cycle). Learning includes explicit cognitive predictions as well as implicit classical and operant conditioning (Kringelbach and Berridge, 2009). Leptin, ghrelin, and serotonin have been implicated, among others, in satiation and satiety (de Graaf et al., 2004; Voigt and Fink, 2015; Cassidy and Tong, 2017). It has been suggested that social rewards are processed at the same reward network as nonsocial rewards and addiction (Wang and Aragona, 2004; Young and Wang, 2004; Krach et al., 2010; Liu et al., 2010).

In the following subsections, we are going to review in more detail what methodological and technical advancements have been achieved and what positive-emotion measures have been identified so far in dogs' positive-emotion perception, processing, and response assessment. We start with behavioral measures, including research on brain lateralization of emotion processing, facial expression analysis, and qualitative approaches. Thereafter, we discuss specific noninvasive physiological and endocrine measures applied in positive-emotion assessment. Finally, we discuss neurobiological methods applied in dog emotion research.

Behavioral Measures

Behavioral signals play an important role in intra- and interspecies emotional communication. Expressing emotions through facial and body movements has been documented in several studies (Beerda et al., 1997, 1998; Rehn and Keeling, 2011; Shiverdecker et al., 2013). However, some of the behavioral indicators mentioned below have been associated with both negative and positive-emotions.

Thus far, research has focused mainly on identifying behaviors associated with negatively connotated emotions. Although there exists a high within-individual variability in behavior expression, behaviors such as increased activity, repetitive movements, auto-grooming, lowered body posture, lip licking, panting, yawning, crouching, shaking, vocalization (barking, whining), scratching, paw lifting, paw sweating, increased salivation, blinking of eyes have been identified as stress indicating behaviors in dogs (Hetts et al., 1992; Beerda et al., 1997, 1998, 1999; Dreschel and Granger, 2005; Tod et al., 2005; Hennessy et al., 2006; Siniscalchi et al., 2008; Stracke et al., 2011; Hekman et al., 2012; Shiverdecker et al., 2013; Kuhne et al., 2014b; Csoltova et al., 2017).

On the other hand, increased physical activity (Rehn and Keeling, 2011; McGowan et al., 2014), attentive behavior (Rehn and Keeling, 2011; Westerback, 2011), tail wagging (Rehn and Keeling, 2011; Takahashi, 2011; McGowan et al., 2014), lip licking (Rehn and Keeling, 2011; Westerback, 2011; Gygax et al., 2015), vocalization, and shake off (Rehn and Keeling, 2011) have been associated with positive-emotional states in dogs.

Vocalization

Dogs use a wide range of different context-specific subunits of barks and mixed sounds as a means for communication of emotional arousal and both positive and negative emotional states. However, high variability has been found among, as anywhere from 2 to 12 types of subunit barks were identified in different breeds (Feddersen-Petersen, 2000), consisting of acoustic parameters such as frequency, tonality, and rhythmicity (Pongrácz et al., 2010).

Apart from intraspecies communication, research also shows that dogs' barking represents an important active communication tool also with humans (Feddersen-Petersen, 2000; Yin, 2002; Pongrácz et al., 2005, 2006). In addition, humans seem to be able to correctly identify the emotional state of the dog based on context-specific barks. Short inter-bark time lapses are perceived as aggressive, while longer time lapses between barks indicate low aggression. Higher pitched barks combined with longer between bark sequences are associated with happiness and playfulness (Yin and McCowan, 2004; Pongrácz et al., 2005, 2006). However, excessive barking has been linked to the excitement, boredom, disturbances, anxiety, and pain in dogs (Righetti, 2005).

Whining and yelping sounds were recorded when the owner returned after separation, suggesting increased positive arousal and motivation to approach the owner (Rehn et al., 2014). Another study found that early onset of whining after short separation from the owner was the most typical vocal response of dogs diagnosed with a separation-related disorder. According to the authors of the study, barking encompasses a wide range of both positive and negative emotional states, while, on the other hand, whines are more associated with negative emotions (Pongrácz et al., 2017).

Activity

Activity, in a form of exploration or information gathering, might be a relevant indicator of the animal's well-being (Boissy et al., 2007). Increased activity was shown as a sign of positive excitement in dogs when reunited with the owner after separation (Rehn et al., 2014) or when the dogs were solving a cognitive task (McGowan et al., 2014). On the other hand, this behavioral indicator is also context specific, since excitation was also documented as an indicator of moderate stress in a social setting (Beerda et al., 1998, 2000) and shelter environment (Part et al., 2014; Cozzi et al., 2016).

However, activity measured as speed or latency to approach food in subsequent runway tests might be a relatively easy and effective tool to measure incentive salience in dogs. The operant runway method has been proved to be a useful approach to study the behavioral and neurobiological basis of reward-seeking motivation in rodents (Hull, 1934; Crespi, 1942; Ettenberg, 2009). Research suggests that the time necessary to cross the runway is a reliable indicator of the animal's incentive salience (Ettenberg, 2009). The runway method may, therefore, be an interesting alternative for exploring food-related behavior in dogs.

Recently, two studies implemented the runway task as a tool to test its usefulness in food preference in dogs. Both research groups found that dogs moved faster through the runway to obtain a more preferred food compared to the less preferred food (Riemer et al., 2018; Cameron et al., 2019). However, the food quantity did not affect the running speed, suggesting a higher incentive value of the more preferred food over a greater quantity of less preferred food (Riemer et al., 2018).

Lip Licking

Observed higher frequencies of oral behavior in a form of lip/nose licking and/or tongue flicking have previously been proposed to indicate acute stress in a social context (e.g., Beerda et al., 1997, 1998; Csoltova et al., 2017). Nose licking has been also observed in frustration-provoking situations when access to a food reward was denied to dogs (Bremhorst et al., 2019).

Albuquerque et al. (2018) studied dogs' lip licking responses to both positive and negative stimuli. They have found more prevalent frequency of lip licking in response to negative visual stimuli (human's and dogs' angry and aggressive facial expressions) compared to positive ones (humans' and dogs' happy and playful expressions). In addition, authors have found higher rates of lip licking in response to human stimuli.

On the other hand, other research findings suggest that lip licking could be associated with positive-emotion, performed in response to verbal and physical human interactions and seeing an owner after separation (Rehn and Keeling, 2011; Westerback, 2011; Gygax et al., 2015).

Tail Wagging

A higher frequency of tail wagging recorded in social settings has been proposed as an indicator of emotion reflecting positive valence and contact-seeking behavior (Rehn and Keeling, 2011; Rehn et al., 2014). Tail wagging related to positive expectation was observed during treat offerings (Travain et al., 2016). Also, dogs were observed to wag their tails more as a reaction toward food reward or human contact and less to conspecifics (McGowan et al., 2014).

Play Behavior

Play behavior is a pleasurable experience and thus a possible indicator of a positive-emotional state. Play behavior includes a complex set of different motor activities and play patterns. Through play, dogs acquire specific skills necessary for survival (Bekoff, 1974a). Social play has an important role in developing social experiences and skills (Bekoff, 1974b, 1984). The high prevalence of social play in adult dogs indicates its social cohesion and bonding function (Bradshaw et al., 2015; Palagi et al., 2015; Sommerville et al., 2017). In addition, it was found that the affiliative behavior of the human handler during play decreased cortisol levels in working dogs (Horváth et al., 2008).

However, there have been some debates regarding whether play behavior is a reliable indicator of positive welfare since the play occurs under less favorable environmental conditions as well (Held and Špinka, 2011; Sommerville et al., 2017).

Behavioral Lateralization of Emotion Processing

Extensive evidence exists about brain lateralization in perception and response to emotion-eliciting stimuli in different animal species (e.g., Fernández-Carriba et al., 2002; De Boyer Des Roches et al., 2008; Rogers, 2010; Wallez and Vauclair, 2011; Leliveld et al., 2013; Rogers et al., 2013; Siniscalchi et al., 2016c). The main existing brain lateralization theories propose different explanations of emotional processing. The right hemisphere hypothesis states that the right cerebral hemisphere dominates the perception and regulation of emotional processes independent of the emotion valence (Borod et al., 1998). On the other hand, the valence-specific hypothesis suggests that each cerebral hemisphere is responsible for different emotional valence perception and processing, with the left hemisphere being dominant in positively connotated emotion processing, while the right hemisphere predominantly processes negative emotions, such as fear and aggression (Ahern and Schwartz, 1979; Wedding and Stalans, 1985; Adolphs et al., 2001).

In the following subsections, we review research done on behavioral lateralization of emotion processing, including emotional information perception and emotional expression.

Visual lateralization

Emotional facial expressions communicate one's desires and intentions and may influence others' emotional state. Therefore, they play an important role in social interactions. The animal's ability to accurately recognize and discriminate emotional information, including the facial emotions of others, is a core element of social competence promoting adaptive behavior in response to perceived information (Lindell, 2013).

Research evidence exists that dogs are capable of facial recognition (Racca et al., 2010; Somppi et al., 2014). In addition, further studies revealed pronounced specificities regarding facial processing, demonstrating dogs' ability to discriminate between different emotional facial expressions in humans (Nagasawa et al., 2011; Müller et al., 2015; Turcsán et al., 2015; Somppi et al., 2016). Besides, dogs looked significantly longer at both human and dog faces whose facial expression reflected the same emotional valence as the vocalization. These results suggest that dogs' brains process, differentiate, and integrate multimodal sensory inputs of different emotional valence (Albuquerque et al., 2016).

Apart from dogs' ability to recognize individual faces visually and discriminate among different emotional states, further studies also revealed gaze bias and lateralized cerebral hemispheric processing of facial expressions. Strong left-gaze bias was recorded in dogs toward images of human faces, but not toward images of monkeys, dogs, and inanimate objects (Guo et al., 2009). Further study revealed that dogs looked significantly more into the right side of the face, regardless of the emotion expressed in their left visual field, indicating the right cerebral hemispheric dominance for processing all emotions. Facial expressions depicting positive-emotion resulted in forehead gaze fixation, while gaze fixation on the eye and mouth region was recorded in response to negative facial expression (Barber et al., 2016).

Within the framework of the valence-specific hypothesis, left-gaze bias was observed in dogs in response to pictures depicting negative facial expressions of conspecifics and a right-gaze bias in response to positive expressions. No gaze bias was observed in response to neutral dog facial expressions. In response to pictures depicting human facial expressions, the right cerebral dominance (left-gaze bias) was found in response to negative and neutral expressions; however, no gaze bias was recorded toward positive expressions (Racca et al., 2012).

In a different study, human facial expressions depicting the same emotion (happiness, surprise, disgust, fear, sadness, anger, or neutral) were simultaneously presented into the left and right visual fields of the dog during feeding. Faces depicting anger, fear, and happiness resulted in left-turn bias, while surprise facial expression resulted in right head-turn bias. Shorter head-turning reaction time was recorded for fear and anger facial expressions in comparison with other emotional stimuli. For the facial expression depicting disgust and the neutral facial expression, no head-turning bias was observed. Further, angry human facial expressions resulted in longer latency to resume eating compared to other emotional facial expressions. Increased stress-associated behavioral responses to angry and happy human facial expressions were observed. Lastly, fearful, angry, and happy emotional expressions resulted in significantly higher cardiac activity in dogs, indicating dogs' sensitivity to human emotional facial expression (Siniscalchi et al., 2018).

Apart from studies on dogs' lateralized emotional facial-expression perception, lateralized head-orienting responses were observed to other visual emotion-eliciting stimuli in dogs as well. Silhouettes depicting a dog, a cat, or a snake were simultaneously presented into the left and right visual hemifields of the dog while feeding. Cat and snake pictures resulted in a left head-turning bias and shorter reaction time, suggesting right hemispheric activation for threatening and alarming stimuli. No head-turning bias was observed for a silhouette of the dog. When stimuli were presented either to the left or right visual spaces, dogs were found to react more to the left than to the right-side presentations, regardless of the stimulus presented. Furthermore, both left head-turning bias and the presentation of a cat and a snake silhouettes into the left visual space required a longer latency to resume feeding (Siniscalchi et al., 2010).

Acoustic lateralization

It seems that dogs are able to differentiate between positive (laughing) and negative (crying) emotional auditory stimuli (Huber et al., 2017), and additional research has revealed contra-lateralized brain processing in response to human emotional vocalization (Siniscalchi et al., 2008). In particular, the analysis of human nonverbal vocalizations showed a clear left head-orienting toward negative emotional stimuli (fear and sadness), suggesting a prevalent activation of the right cerebral hemisphere. On the contrary, a clear right head-turning response was recorded in response to positive vocalization (happiness), suggesting dominant left cerebral hemisphere activation in dogs. Moreover, heart rate and behavioral responses have provided further confirmatory evidence that human emotional sounds induced emotional responses in dogs (Siniscalchi et al., 2008).

Olfaction lateralization

Contrary to other senses, olfactory information projects predominantly to the ipsilateral hemisphere, meaning that right nostril sensory input is processed mainly in the right cerebral hemisphere, while the left cerebral hemisphere processes mainly the input from the left nostril (Royet, 2004). Previous research on dogs' olfactory behavior has found nostril bias when investigating and processing odors (Siniscalchi et al., 2011, 2016b; Brown and Reimchen, 2020). Novel and non-aversive stimuli resulted in an initial right nostril sniffing preference, followed by a switch to left nostril investigation during repeated exposures. Consistent right-nostril sniffing bias was observed for potentially arousing emotional stimuli such as the sweat of a veterinarian and adrenaline (Siniscalchi et al., 2011). The right nostril bias, in response to novel and arousal stimuli, suggests sympathetic activation, which is predominantly controlled by the right cerebral hemisphere (Craig, 2005).

Asymmetric nostril use was also observed in response to human and canine odors produced during emotional states such as joy, fear and anxiety, physical stress, and neutral stimuli. Right nostril bias was observed when dogs investigated conspecific stress-indicating odors (collected when the dog was isolated in an unfamiliar environment). Left nostril bias was documented when dogs sniffed human odors produced during fear and physical stress (running). These results, according to the authors, indicate that dogs might use different sensory pathways for conspecific versus heterospecific emotional signals processing (Siniscalchi et al., 2016b).

Facial expression lateralization

A study examining facial expression lateralization in dogs in response to positive social stimuli (the owner) found that dogs moved their left eyebrow more after reuniting with the owner compared to the baseline. No facial expression bias was recorded for positive nonsocial stimuli (such as a dog toy). The authors have concluded that the left eyebrow bias most probably reflects dogs' attachment to the owner (Nagasawa et al., 2013).

Motor lateralization

Rapidly growing empirical research suggests evidence also for motor lateralization in dogs. Researchers have found a link between the paw and visuospatial preference. Left-pawed dogs were found to consume more food kibbles on the left side of the feeding apparatus and similarly, right-pawed dogs ate more of the food on the right side of the feeding apparatus. Ambidextrous dogs did not show any bias. This evidence indicates an association between motor laterality and visuospatial bias in dogs, similar to the one found in humans (Siniscalchi et al., 2016a).

Interesting findings have been reported from a study investigating the association between motor laterality, emotional state, and cognitive bias in dogs. The emotional state was assessed by a cognitive test assessing dogs' food-approach latency. The food bowl was positioned in one of three ambiguous positions. According to the study, the distributions of lateralized (57%) and non-lateralized (43%) dogs were roughly equal. It was found that left-pawed dogs tended to be more negative in their cognitive processing than right-pawed or ambidextrous conspecifics. The study proposes that paw preference, as an indicator of hemispheric dominance, can reliably predict cognitive bias in dogs and can therefore represent a quick and useful prevention tool to identify animals that are at risk from negative welfare, thus enabling quick interventions to improve their well-being (Wells et al., 2017).

Research studies are suggesting that bilateral asymmetry of tail-wagging is also related to the valence of emotional stimuli (Quaranta et al., 2007; Artelle et al., 2011; Siniscalchi et al., 2013). Differential amplitudes of lateral asymmetry of tail wagging were found in response to the type of emotion-eliciting visual stimuli the dogs were presented with. Dogs presented with stimuli eliciting approach motivation (seeing dog's owner) performed higher amplitude of right-side tail wagging. By contrast, stimuli associated with withdrawal motivation (dominant unfamiliar dog presentation) resulted in a higher amplitude of left-side tail wagging (Quaranta et al., 2007).

According to the findings, dogs not only respond with asymmetric tail wagging to qualitatively different emotional stimuli (Quaranta et al., 2007) but are also sensitive to the asymmetric tail wagging displayed by conspecifics (Artelle et al., 2011). Higher cardiac activity and anxiety-indicating behavior were recorded when dogs watched left-side tail wagging compared to right-side tail wagging video recordings of conspecifics (Siniscalchi et al., 2013).

Facial Expression Analysis

A facial expression is nonverbal communication that has both survival and adaptive function (Erickson and Schulkin, 2003). Most nonhuman animals produce an automatic involuntary display of facial expressions in response to specific emotion-eliciting stimuli. Lately, there has been an increase in the number of studies on the facial expression of pain in different animal species (Langford et al., 2010; Sotocina et al., 2011; Keating et al., 2012; Costa et al., 2014; Holden et al., 2014; Guesgen et al., 2016; McLennan et al., 2016; Finka et al., 2019). Further, it has been proposed that facial expression may reliably indicate both negative and positive-emotional states and thus have a substantial potential in animal welfare assessment (Descovich et al., 2017).

One of the methods used, to noninvasively measure human muscle movements is called the Facial Action Coding System—FACS (Ekman and Rosenberg(eds), 2005). This research tool enables the user to manually code almost any anatomically possible facial expression. To identify and code facial movements in nonhuman species, AnimalFACS was developed and adapted from the original human FACS. This coding system facilitates intra-species and inter-species comparisons of facial expressions (Vick et al., 2007; Parr et al., 2010; Waller B. M. et al., 2012; Caeiro et al., 2013, 2017a; Micheletta et al., 2015; Wathan et al., 2015).

Research has documented that domesticated dogs have developed facial muscles, enabling facial expression of emotion, unlike their wolf ancestors (Waller B. M. et al., 2013; Kaminski et al., 2019). DogFACS has been used to study dog facial expressions in response to different emotional stimuli and compare them with human facial expressions (Waller B. et al., 2013). Emotional stimuli eliciting happiness (such as initiation of play with the owner), positive anticipation (related to food and outdoor activity), frustration (inaccessible toy, food, or space), and fear (experience of a thunderstorm or visualization of specific objects) were used. Researchers identified distinctive stimuli-dependent facial expressions in dogs, although these expressions differed from human facial expressions in response to categorically similar emotional stimuli (Caeiro et al., 2017b).

Research groups studying hedonic and aversive reactions toward taste stimuli found homologous inter-species facial expressions. The results revealed similar distinctive facial expressions in response to sweet and bitter taste stimuli, as well as in the intensity of the emotional reaction (Grill and Norgren, 1978; Berridge et al., 1981; Berridge, 2000; Steiner et al., 2001). Thus far, dogs have not been observed to display specific facial expressions in response to palatable food; however, an increase in "ears adductor" has been observed during anticipation of food reward (Bremhorst et al., 2018).

Qualitative Behavioral Assessment

In recent years, qualitative methods to assess animal emotion and welfare have been gaining more and more attention (e.g.,Wemelsfelder et al., 2000; Wemelsfelder and Farish, 2004; Knierim and Winckler, 2009; Walker et al., 2010;

Stockman et al., 2011; Rutherford et al., 2012; Fleming et al., 2013; Wemelsfelder and Mullan, 2014; Konok et al., 2015b).

Qualitative Behavioral Assessment (QBA) is a holistic, noninvasive, positive, and dynamic method using fixed lists of descriptors to measure emotional expressivity in different animal species (Wemelsfelder, 2007; Wemelsfelder and Mullan, 2014). In this assessment, the trained observer integrates multiple quantitative behavioral responses to describe the animal's emotional state qualitatively. QBA has been used to assess the dogs in the shelter and home environments (Walker et al., 2016; Arena et al., 2019). Most recently, a fixed list of qualitative descriptive terms containing both positive (e.g., playful, curious, relaxed, tranquil) and negative (e.g., bored, apathetic, fearful, wary) connotations has been developed as a complementary assessment tool to evaluate the welfare of dogs in a shelter environment (Arena et al., 2019).

Noninvasive Physiological and Endocrine Measures

There exists a close relationship between emotions and physiology, more particularly the autonomic nervous system (ANS) and the hypothalamic-pituitary-adrenal (HPA) axis activity (Sander and Scherer, 2014). Therefore, biomarkers play an important role and serve as a proxy when assessing emotion and positive well-being in animals (e.g.,von Borell et al., 2007; Schmied et al., 2008, 2010; Reefmann et al., 2009a,b; Coulon et al., 2013, 2015; Briefer et al., 2015; Kowalik et al., 2017). Heart rate (HR) (Csoltova et al., 2017), heart rate variability (HRV) (Bergamasco et al., 2010; Katayama et al., 2016; Travain et al., 2016), surface temperature (Travain et al., 2015, 2016; Csoltova et al., 2017), oxytocin (Odendaal and Meintjes, 2003; Mitsui et al., 2011; Rehn et al., 2014; Nagasawa et al., 2015), vasopressin (Hydbring-Sandberg et al., 2004; MacLean et al., 2017a,b, 2018; Pirrone et al., 2019), cortisol (Hennessy et al., 1998, 2006; Coppola et al., 2006; Bergamasco et al., 2010; Shiverdecker et al., 2013), and alpha-amylase (Contreras-Aguilar et al., 2017; Hong et al., 2019) have been implemented and showed potential usefulness in indirect and noninvasive assessment of positive-emotion in dogs.

Heart Rate

Monitoring HR responses has been utilized as an effective way for assessing the sympathetic branch activity of ANS activation in both animal and human studies (e.g., Beerda et al., 1998; Watkins et al., 1998; Loijens et al., 2002; Cyr et al., 2009; Csoltova et al., 2017). Itis widely accepted that measurements of HR are valid indicators of ANS activity and thus arousal and stress response (Ulrich-Lai and Herman, 2009). Although HR has been reported as a reliable indicator of arousal during behavioral tests, it is suggested that it cannot be used as an indicator of emotional valence (Beerda et al., 1998; Lensen et al., 2017).

Besides emotions, HR may be affected by different factors, for example, physical activity and temperature (Hales and Dampney, 1975; Maros et al., 2008). In dogs, it has been found that walking increased HR, which decreased during lying, although no differences in HR were found between sitting and standing (Maros et al., 2008).

Positive human-dog tactile contact has been shown to have an attenuating effect on cardiovascular responses of the dog (Anderson and Gantt, 1966; Lynch and McCarthy, 1967; McGreevy et al., 2005; Handlin et al., 2011; Csoltova et al., 2017; McGowan et al., 2018). In addition, the sole presence of the owner during a threatening situation has proved to have a stress-buffering effect on dogs' HR, thus providing evidence for the "safe haven" effect of the owner on a dog's well-being during a stressful situation (Gácsi et al., 2013).

Besides, HR monitoring was implemented when testing the hedonic aspects of food in dogs. Eating food was associated with initial increased cardiac activity, with a gradual return to baseline levels. The heart rhythm was found to be affected by the palatability of the food, with the most profound increase and decrease observed in response to the most preferred food (Kostarczyk and Fonberg, 1982). Similarly, a significant increase in HR was also observed when the dogs were offered a tasty treat (Travain et al., 2016).

Heart-Rate Variability

HRV has been shown to be an effective tool to measure the sympathetic and parasympathetic balance of the ANS (van Ravenswaaij-Arts, 1993; Thayer et al., 2010). HRV reflects variance in time intervals in successive heartbeats, indicating the organism's capacity to regulate internal and external demands (van Ravenswaaij-Arts, 1993; Jarczok et al., 2015; Mccraty and Shaffer, 2015; Shaffer and Ginsberg, 2017).

There have been three approaches commonly utilized to monitor HRV (van Ravenswaaij-Arts, 1993; Electrophysiology Task Force of the European Society of Cardiology the North American Society of Pacing Electrophysiology, 1996; Shaffer and Ginsberg, 2017; Young and Benton, 2018; **Table 1**):

1. Time-domain measurements (linear analysis) record the variability of the successive heartbeats during the measured time periods. They include parameters such as mean RR, SDRR/SDNN, RMSSD, NN50, and pNN50 (Shaffer and Ginsberg, 2017; Drury et al., 2020).
2. Frequency-domain (linear analysis) measure the absolute or relative power (the signal energy) distribution to different frequency bands such as ULF, VLF, LF, and HF (Electrophysiology Task Force of the European Society of Cardiology the North American Society of Pacing Electrophysiology, 1996; Shaffer and Ginsberg, 2017; Drury et al., 2020).
3. Nonlinear measures estimate the unpredictability and irregularity of time series (Stein and Reddy, 2005; Shaffer and Ginsberg, 2017; Young and Benton, 2018). They include, for example, SD1, SD2, ApEn, SampEn, DFA $\alpha1$, DFA $\alpha2$, and D2 parameters.

Assessing canine emotional states by implementing HRV indices has been gaining research popularity in recent years (Bergamasco et al., 2010; Gácsi et al., 2013; Bowman et al., 2015; Katayama et al., 2016; Travain et al., 2016; Zupan et al., 2016; McGowan et al., 2018; Köster et al., 2019). It has been proposed that HRV parameters might be sensitive indicators of emotional

TABLE 1 | Description of HRV measures (adapted from Electrophysiology Task Force of the European Society of Cardiology the North American Society of Pacing Electrophysiology, 1996; Shaffer and Ginsberg, 2017).

		Parameter	Unit	Description
Heart-rate variability	Time-domain measures	mean RR	ms	The mean of RR intervals
		SDRR/SDNN	ms	The standard deviation of RR/NN intervals
		RMSSD	ms	Root mean square of successive RR interval differences
		NN50		Number of successive NN intervals that differ more than 50 ms
		pNN50	%	Percentage of successive NN intervals that differ by more than 50 ms
	Frequency-domain measures	ULF	ms^2	The absolute power of the ultra-low-frequency band (≤0.003 Hz)
		VLF	ms^2	The absolute power of the very-low-frequency band (frequency range 0.0033–0.04 Hz)
		LF	ms^2	The absolute power of the low-frequency band (frequency range 0.04–0.15 Hz)
		LF	n.u.	The relative power of the low-frequency band (frequency range 0.04–0.15 Hz) in normalized units
		HF	ms^2	The absolute power of the high-frequency band (frequency range 0.15–0.4 Hz)
		HF	n.u.	The relative power of the high-frequency band (frequency range 0.15–0.4 Hz) in normalized units
		LF/HF	ms^2	The ration between LF and HF band powers
	Nonlinear measures	SD1	ms^2	Poincaré plot representing the standard deviation perpendicular to the line of identity (the standard deviation of instantaneous beat-to-beat R-R interval variability) (Tulppo et al., 1996)
		SD2	ms^2	Poincaré plot representing the standard deviation along the line of identity (the standard deviation of continuous long-term R-R interval variability) (Tulppo et al., 1996)
		ApEn		Approximate entropy, quantifying the regularity and complexity of a time series (Pincus et al., 1991)
		SampEn		Sample entropy estimates the regularity and complexity of a time series (Richman and Moorman, 2000)
		DFA α1		Detrended fluctuation analysis, reflecting short-term fluctuations (Peng et al., 1995; Ho et al., 1997)
		DFA α2		Detrended fluctuation analysis, reflecting long-term fluctuations (Peng et al., 1995; Ho et al., 1997)
		D_2		Correlation dimension measures the minimum number of variables required to construct a model of system dynamics

RR, inter-beat intervals between all successive heartbeats; NN, normal inter-beat intervals between all successive heartbeats (removed abnormal beats/artifacts) (Electrophysiology Task Force of the European Society of Cardiology the North American Society of Pacing Electrophysiology, 1996; Shaffer and Ginsberg, 2017; Drury et al., 2020); ms, milliseconds; %, percentage; ms^2, meter per second squared; n.u., normalized units calculated; LF [n.u.] = LF [ms^2] / (total power [ms^2] – VLF [ms^2]); HF [n.u.] = HF [ms^2] / (total power [ms^2] – VLF [ms^2]); Hz, hertz.

valence (Katayama et al., 2016) and tend to be less affected by physical activity compared to HR (Maros et al., 2008).

Positive-emotion-eliciting stimuli, such as food, human-dog interaction, and listening to music, all resulted in changes of HRV parameters in dogs (Bergamasco et al., 2010; Bowman et al., 2015; Travain et al., 2016; Zupan et al., 2016; McGowan et al., 2018).

An increase in RMSSD, pNN50, and HF parameters has been reported as an indicator of a positive-emotional state in dogs after 15 min of physical contact with humans (McGowan et al., 2018).

Exposure to auditory stimuli in the form of classical music resulted, among others, in mean RR, STDRR, RMSSD, pNN50, SD1, SD2 increase, and LF/HF decrease, indicating parasympathetic nervous system dominance and stress-buffering effects of music on dogs in a stressful environment (Bowman et al., 2015; Köster et al., 2019).

Zupan et al. (2016) studied the effects of positive stimuli on cardiac responses in dogs using higher- versus lower-valued food and social reward (familiar and less familiar person). Positive stimuli resulted in an increase of HR and LF/HF ratio, implying sympathetic nervous system activation and a positive arousal state in dogs throughout testing. In contrast to the aforementioned studies, exposure to the positive stimuli resulted in RMSSD and HF decrease compared to the baseline. A similar decrease was recorded for the LF compared with the baseline. A decrease in HF was observed when dogs were offered more preferred food (meatball) compared to less preferred food (commercial kibbles). A decrease in HF and RMSSD was recorded during the reward phase when the dog was allowed to interact with a person or eat the food compared to the anticipation phase when the dogs could only see the rewards. Authors proposed that higher positive-emotional valence in dogs is associated with parasympathetic deactivation. In this regard, lower RMSSD and HF combined are indicators of higher valence in an already positive-emotional state.

Interestingly, a negative experience in the form of isolation in an unfamiliar environment also resulted in RMSSD decrease in dogs. On the other hand, a decrease in SDNN was recorded when the dogs were petted by their owners (Katayama et al., 2016).

In another study, decreased SDNN has been linked to elevated attention, recorded when the dogs focused on their favorite ball (Maros et al., 2008).

When investigating cardiac responses to food treats during appetitive and reward phases, the authors found an increased HR, although no changes in HRV parameters were recorded. A significant increase in SDNN was observed after the positive stimulation occurred, during the post-consumption phase (Travain et al., 2016).

Superficial Temperature

Both positive and negative emotions activate ANS responses, which subsequently lead to physiological changes associated with alterations of blood flow, leading to surface temperature fluctuations (Sinha et al., 1992; Collet et al., 1997; Chotard et al., 2018).

Implementation of infrared thermography (IRT) is an effective way to accurately quantify the smallest superficial temperature changes in response to environmental and psychological stimuli, both in humans (Pavlidis et al., 2000, 2002; Pollina et al., 2006; Goulart et al., 2019; Panasiti et al., 2019; Zhang et al., 2019) and animals (Mccafferty, 2007; McManus et al., 2016; Telkanranta et al., 2018). IRT is a noninvasive imaging technique that detects the infrared wavelengths emitted by all objects with a temperature above absolute zero (Vollmer and Möllmann, 2017). Thermographic cameras provide a tool to monitor sudden rises and decreases in superficial temperature by either real-time observations or ultrahigh-speed video or thermal image recordings of studied objects.

In general, areas without the interference of fur are used as regions of interest to detect heat changes. Eye (Stewart et al., 2008; Csoltova et al., 2017) and nose (Kuraoka and Nakamura, 2011; Proctor and Carder, 2016) temperatures are used most frequently, but other body parts, such as the ears (Riemer et al., 2016) have also been used as a region of interest when studying emotion-induced heat surface changes in animals.

Due to the recent advances in thermal imaging technology and its noninvasive noncontact nature, the use of portable infrared cameras in animal emotion assessment research has been gaining popularity (e.g., Nakayama et al., 2005; Stewart et al., 2005, 2007, 2008, 2011, 2017; Kuraoka and Nakamura, 2011; Valera et al., 2012; Bartolomé et al., 2013; Herborn et al., 2015; Proctor and Carder, 2015; Cannas et al., 2018; Chotard et al., 2018; Hussein, 2018; Redaelli et al., 2019).

In dogs, there has been a growing interest in utilizing IRT to investigate negative emotion-induced surface heat increase associated mainly with stress, fear-based aggression, and separation anxiety, both in clinical and home settings (Travain et al., 2015; Riemer et al., 2016; Csoltova et al., 2017; Rigterink et al., 2018).

The affiliative behavior of the owner during a veterinary examination was found to have an attenuating effect on maximal ocular surface temperature compared to the no-interaction condition, reflecting possible parasympathetic activation (Csoltova et al., 2017).

The reappearance of both familiar and unfamiliar persons after a brief separation was sufficient to increase dogs' outer ear temperature (Riemer et al., 2016).

The increase of maximal eye temperature was also recorded when dogs were anticipating and eating treats offered by owners (Travain et al., 2016).

From the research carried out so far, it is possible to conclude that IRT is a useful method to assess arousal intensity (Csoltova et al., 2017), but there has been some debate about whether IRT can distinguish emotional valence (Travain et al., 2015, 2016).

Oxytocin

Oxytocin is a neuropeptide and biomarker that is associated with a positive-emotional state in dogs (Mitsui et al., 2011).

Besides, previous studies indicate that in dogs, oxytocin may regulate a dog's social behavior and attachment toward the owner (Beetz et al., 2012; Romero et al., 2014; MacLean and Hare, 2015; Nagasawa et al., 2015; Buttner, 2016; Kis et al., 2017; MacLean et al., 2017a). It seems that the sole reappearance of a familiar person, following separation, is sufficient to increase dogs' oxytocin levels, but tactile and verbal contact is required for the oxytocin levels to remain continuously elevated (Rehn et al., 2014). Another study assessing the effect of positive human-dog interaction, found increased concentrations of biomarkers such as b-endorphin, oxytocin, prolactin, β-phenylethylamine, and dopamine in both humans and dogs (Odendaal and Meintjes, 2003). Similarly, other studies have supported the association between positive human-dog physical interaction and an increase in oxytocin in dogs (Handlin et al., 2011; MacLean et al., 2017a; Ogi et al., 2020).

Feeding and food-associated stimuli were equally found to increase oxytocin levels in dogs (Uvnäs—Moberg et al., 1985).

Moreover, the administration of exogenous oxytocin has been shown to have a pronounced effect on dogs' cognition and behavior. Intranasal oxytocin administration increased the positive expectation of the dogs in the cognitive bias test (Kis et al., 2015), reduced separation anxiety (Thielke and Udell, 2017), and enhanced performance in a cognitive task (Oliva et al., 2015). Likewise, intranasal oxytocin administration increased dogs' play motivation and intra- and interspecific social play behavior (Romero et al., 2014). Further, intranasally administered oxytocin has been shown to affect cardiac activity by decreasing HR and increasing HRV in dogs (Kis et al., 2014).

Urinary and, most recently, salivary oxytocin sampling has been validated as noninvasive approaches for quantifying oxytocin levels in dogs (Mitsui et al., 2011; MacLean et al., 2018; Powell et al., 2019; Schaebs et al., 2019; Wang et al., 2019).

However, as reported by Rault et al. (2017), it is still too early to consider oxytocin a potential indicator of positive well-being and/or welfare, given the discrepancies in the methodologies used to measure oxytocin in domesticated animals.

Vasopressin

Arginine vasopressin (AVP) is a neuropeptide closely related to oxytocin (Baribeau and Anagnostou, 2015). Both biomarkers play an important role in regulating mammals' social and affiliative behavior (including pair-bonding and maternal behavior), social cognition, social stress and anxiety, and social aggression (Kendrick et al., 1997; Carter, 1998; Everts and Koolhaas, 1999; Goodson and Bass, 2001; Young and Wang, 2004; Donaldson and Young, 2008; Heinrichs and Domes, 2008; Veenema et al., 2010; Bisagno and Lud Cadet, 2014; Baribeau and Anagnostou, 2015).

In dogs, vasopressin increase has been associated with acute stress responses (Hydbring-Sandberg et al., 2004) and was also reported in dogs with separation anxiety (Pirrone et al., 2019). Further, lower free, but higher total plasma AVP has been found in aggressive dogs (MacLean et al., 2017b).

On the other hand, positive affiliative human-dog interactions, such as physical contact play, licking, lying supine have been associated with oxytocin increases, and AVP decreases (MacLean et al., 2017a).

Apart from blood sampling, salivary AVP has been validated as a potential noninvasive biomarker in dogs (MacLean et al., 2017b, 2018).

Cortisol

Increased cortisol levels are associated with HPA axis activation (Romero and Butler, 2007). Testing salivary cortisol levels in dogs has become a well-established method for measuring stress response and its impact on dogs' well-being in several settings (Beerda et al., 1996, 1998; Dreschel and Granger, 2005; Haubenhofer and Kirchengast, 2006; Hekman et al., 2012; Glenk et al., 2014; Ng et al., 2014). Differences in the intensity and nature of a given stressor may impact endocrine responses, thus affecting cortisol release. A time frame from 10 to 30 min is required in order to detect a significant rise in cortisol concentrations in saliva after the onset of an acute stressor (Vincent and Michell, 1992; Beerda et al., 1998). To avoid the impact of handling on the measured cortisol concentration, the saliva sample collection time should not exceed 4 min (Kobelt et al., 2003).

There exists evidence suggesting an inverse relationship between cortisol and positive-emotional state in humans (Lindfors and Lundberg, 2002; Lai et al., 2005). Decreased cortisol levels have been implemented as an indicator of the stress-buffering effect of stimuli in several dog welfare studies. Such positive effects have been observed in human-dog interaction and listening to music, as dogs' cortisol levels showed a decrease when studied in an animal shelter (Hennessy et al., 1998, 2006; Coppola et al., 2006; Bergamasco et al., 2010; Shiverdecker et al., 2013) and veterinary environments (Csoltova et al., 2017).

Alpha-Amylase

As with cortisol, measuring decreased levels of alpha-amylase, a crucial salivary enzyme (Nater and Rohleder, 2009), is another noninvasive approach to test sympathetic nervous system deactivation. Salivary alpha-amylase increase in response to both acute and chronic stressors has been documented in different animal species (Fuentes et al., 2011; Behringer et al., 2012; Fuentes-Rubio et al., 2016; Contreras-Aguilar et al., 2018), including dogs (Contreras-Aguilar et al., 2017; Hong et al., 2019). However, other studies emphasize the involvement of the parasympathetic nervous system branch in alpha-amylase secretion (Asking and Proctor, 1989; Nater and Rohleder, 2009; Bosch et al., 2011).

Noninvasive Neurobiological Methods

Increased tendencies to use neurobiological approaches to investigate the canine brain, social intelligence, and emotion have been observed in recent years. Functional magnetic resonance imaging (fMRI) and functional near-infrared spectroscopy (fNIRS) have been implemented to noninvasively study dog brain responses to both positive and negative emotion stimuli (e.g., Andics et al., 2014; Cook et al., 2014, 2016, 2018; Gygax et al., 2015; Berns and Cook, 2016).

Functional Magnetic Resonance Imaging

fMRI is a neuroimaging tool used to measure and quantify brain activity indirectly by detecting dynamic changes in brain tissue oxygenation (Chen and Glover, 2015). Research studies mostly use the fMRI blood oxygen level-dependent imaging (BOLD) method, which reflects changes in blood oxygenation, flow, and volume in response to neural activity (Heeger and Ress, 2002; Glover, 2011; Devlin, 2016).

Thus far, studies using fMRI have focused on identifying neural responses to reward preference, temperament, face, odor, and vocal processing in awakened dogs (Andics et al., 2014; Cook et al., 2014, 2016, 2018; Berns et al., 2015; Dilks et al., 2015).

When studying the neural bases of preferences between social and food reward, researchers found that individual differences in mean ventral caudate activation in response to praise versus food predicted the subsequent behavioral choice between interaction with the owner (verbal praise) and food reward (eat a treat). Interestingly, 13 out of 15 tested dogs showed a preference for praise over food (Cook et al., 2016).

In another study, aggressive temperament was found to positively correlate with amygdala activation in dogs, while watching their caregiver give food to a fake dog. The authors interpret this emotion as a complex, jealousy-like phenomenon (Cook et al., 2018).

Another fMRI study showed that dogs are sensitive to human and dog auditory stimuli of different positive and negative emotional valence. Emotion-eliciting sound signals activated similarly located non-primary auditory areas both in dog and human brains. Besides, more pronounced neural activation was recorded to positive sound stimuli in both humans and dogs (Andics et al., 2014).

Olfactory neuroimaging study with dogs provided evidence for scent discrimination and positive associations with different odors, reflected in the maximal activation of the caudate nucleus to the odor of a familiar human in contrast to the odor of a familiar dog (Berns et al., 2015).

Besides, there is evidence suggesting a relationship between certain canine temperament traits and caudate nucleus activation. Twelve dogs were presented with 15 reward and 15 non-reward signals delivered by a familiar human, an unfamiliar human, or screen projected computer-generated signals during fMRI sessions. Results revealed higher caudate activation for reward versus non-reward signals. Dogs scoring lower on the Canine Behavioral Assessment and Research Questionnaire (C-BARQ) aggressivity trait showed higher caudate activation to the reward than non-reward signals when delivered by a familiar human. On the contrary, in dogs scoring higher on the aggressivity trait, higher differential responses to the reward versus non-reward signals presented by the unfamiliar human and computer projected signals were observed (Cook et al., 2014).

Functional Near-Infrared Spectroscopy

fNIRS is another neuroimaging method and portable equipment used for noninvasive functional mapping of brain activity by using near-infrared detectors to measure cortical concentrations of oxygenation/deoxygenation and hemodynamic changes by absorbing infrared light by hemoglobin (Tamura et al., 1997; Ferrari and Quaresima, 2012).

fNIRS has been used in canine research to assess positive-emotional states during verbal and tactile human interactions. The results revealed that the cortical hemodynamic reaction measured by fNIRS may be a useful indicator of the emotional valence, while measured behavioral responses were shown as useful indicators of arousal level in dogs. The consistency of the hemodynamic frontal cortical reaction throughout the test, in addition to changes in behavioral responses with repetition, indicates that the valence of the stimuli remained the same while the arousal of the dogs decreased as dogs habituated to the repetitions (Gygax et al., 2015).

POSSIBLE FUTURE DIRECTION IN DOG POSITIVE-EMOTION ASSESSMENT

Psychophysiology

Historically, psychophysiology has been interested in studying the impact of emotional processing on physiological functions (Davidson, 2003). With the rapid development of new technologies in the pet care industry, implementing complementary psychophysiology biosensors could shed additional light on our understanding of canine positive-emotions.

Pupil Dilation

Pupil dilation is associated with the interactions of sympathetic and parasympathetic innervations of the ANS in the iris muscle. According to findings in human research, pupil response is a sensitive indicator of emotional arousal, irrespective of the hedonic valence of the stimuli. Pupil dilation was observed during emotionally engaging visual (Bradley et al., 2008) and auditory stimuli (Partala and Surakka, 2003), implying increased sympathetic activation during both pleasant and unpleasant stimuli presentation (Bradley et al., 2008).

It would certainly be interesting to investigate the role of the emotional valence of different types of rewarding stimuli (such as visual, gustatory, olfactory, or auditory stimuli) on pupil dilation in dogs.

Galvanic Skin Response

The galvanic skin response (GSR), also known as the skin conductance response or electrodermal response, is based on continuous autonomic variation in the electrical properties of the skin and results from sympathetic activation when either external or internal stimuli occur that are physiologically arousing (Lykken and Venables, 1971). GSR has been closely linked to autonomic emotional and cognitive processing and reflects sympathetic arousal. It is the only autonomic psychophysiological variable not affected by parasympathetic activity. This method can be implemented in an objective assessment of emotional states and attentional processing (Braithwaite et al., 2013).

GSR was sensitive to stimulus valence in humans presented with pleasant and unpleasant food and nonfood pictures. The pleasant pictures were associated with a decrease in skin conductance, while the negative pictures evoked sweating and increased skin conductance. This indicates the potential effectiveness of GSR in a valence assessment of emotional stimuli (Kuoppa et al., 2016).

In addition, a close relationship between GSR and other psychophysiology measures was found. An accuracy rate of 80.2% was observed between HRV and GSR signals in association with emotion assessment (Lee et al., 2005). High covariation between pupillary dilation and GSR was recorded in reaction to positive and negative picture viewing, suggesting sympathetic nervous system activation in humans (Bradley et al., 2008).

Respiration Rate

Autonomic respiration is regulated by metabolic requirements but can shift in response to changes associated with different emotions, such as sadness, happiness, anxiety, or fear (Homma and Masaoka, 2008). Research on emotion-respiration relationships has largely focused on measuring respiration rate, amplitude, volume, and respiratory cycle (Boiten et al., 1994). In human literature, a study suggests that different emotional states can be differentiated according to the type of breathing pattern (Philippot et al., 2002). In farm animals, the respiration rate seems to be a useful indicator of emotional arousal (Briefer et al., 2015), and possibly also of emotional valence (Reefmann et al., 2009a). Therefore, measuring the respiration rate can shed additional light on emotion processing in dogs.

Immunological Indicators

Many studies on humans found a distinct enhancement effect of positive-emotions on the immune system (Dillon et al., 1986; Pressman and Black, 2012; Stellar et al., 2015). In dogs, only the impact of negative stress on the immune reaction has been studied so far. According to the findings, acute stress affects the immune system by inducing overall peripheral leukocytosis (Beerda et al., 1997). Salivary immunoglobulin A (sIgA) has been proposed as another potentially useful bioindicator of acute and chronic stress in dogs (Skandakumar et al., 1995; Kikkawa et al., 2003).

Association between canine immune system enhancement and positive-emotional state is another research area that requires more attention. Salivary immunological indicators could find their potential usefulness, especially in the assessment of dogs' longer-term emotional states and positive well-being.

Affective Computing in Positive-Emotion Assessment

Both machine learning and deep learning have promising potential in animal behavior, communication, emotion, and welfare research (Valletta et al., 2017; Hantke et al., 2018; Norouzzadeh et al., 2018; Pereira et al., 2019). Machine learning has been used for automatically computing interpretable, quantitative measures and classification of behaviors and activities within complex data sets (Kabra et al., 2013; Dell et al., 2014). Machine learning has been widely applied especially to animal movement and location data analyses (Wang, 2019). In human research, machine learning techniques have already been implemented to recognize emotional states by studying facial expressions (Michel and Kaliouby, 2003), speech (Shami and Verhelst, 2007), body movements and gestures (Castellano et al., 2007), and also physiological responses such as cardiac activity, galvanic skin response, respiration rate, and skin temperature (Shi et al., 2010; Domínguez-Jiménez et al., 2020). Also, infrared thermography data are showing promising usefulness in automatic emotion recognition (Boccanfuso et al., 2016).

Deep learning, a subfield of machine learning, goes further by using a deep neural network to learn from and process raw data (Goodfellow et al., 2015). It has been gaining popularity in human emotion recognition studies (Giannopoulos et al., 2018; Jain et al., 2018; Hassan et al., 2019).

Implementation of affective computing in positive-emotion assessment might be particularly useful where sorting and classifying a large data set are required or where multimodal data integration is necessary to further enhance emotion recognition (Caridakis et al., 2007; Yin et al., 2017). Affective computing might provide solutions in accurate automatic detection of the small subtleties related to different emotional states by analyzing data from either a single biosignal input or by a combination of multiple physiological inputs. Affective computing might also provide solutions for the recognition of emotional states with similar biosignal inputs by analyzing data in a time series (Quesnel et al., 2018). Furthermore, affective computing considerably decreases the time of manual data and video analyses.

In canine emotion research, machine learning has thus far shown promising results in individual, context, and emotion (both valence and intensity) recognition of dog barks (Molnár et al., 2008; Hantke et al., 2018).

Overall, both machine and deep learning offer great potential in automatic emotion detection and recognition (Yin et al., 2017).

THE IMPACT OF HUMAN-DOG RELATIONSHIP ON DOG EMOTION

There is an increasing amount of evidence suggesting that the unique characteristics of the human-dog relationship, owner's personality, emotional state, or behavior have been shown to affect the behavior, cognition, emotion processing, and expression of pet dogs (Prato-Previde et al., 2008; Handlin et al., 2012; Merola et al., 2012; Gácsi et al., 2013; Konok et al., 2015a; Cimarelli et al., 2016; Schöberl et al., 2016; Huber et al., 2017; Dodman et al., 2018; Gobbo and Zupan, 2020; Salamon et al., 2020).

The relationship between owner and dog resembles that of the parent (primary caretaker) and child (Bowlby, 2005). The dog perceives the owner as a secure base from which to explore the world (Topál et al., 1998). Pet owners differ in their attachment style to dogs, and these differences in behavior and emotion toward dogs impact their behavior and emotion toward their dog, subsequently affecting the dogs' interaction with the environment. The owner's attachment and caregiving style have been shown to impact dogs' responses toward stress-inducing stimuli. The dogs of secure owners showed the most independent and confident behavior when they were exposed to environmental stressors compared with dogs of anxious and avoidant owners (Rehn et al., 2017). Moreover, dogs of owners with insecure attachments had a higher tendency to develop separation anxiety (Konok et al., 2015a).

Some studies have found a link between the owner's personality and dogs' behavioral and physiological responses. Owners scoring high in neuroticism and agreeableness had dogs with lower cortisol levels measured in the Strange Situation Test (Schöberl et al., 2016). In addition, dogs pay close attention to owners' responses and act accordingly when facing novel stimuli (Merola et al., 2012; Salamon et al., 2020).

Further, research studies have shown that dogs tend to synchronize their emotional states with their owner (Sümegi et al., 2014; Turcsán et al., 2015; Sundman et al., 2019). Emotional contagion is an immediate synchronization of the emotional state between the subject and an object (Preston and de Waal, 2002; Nakahashi and Ohtsuki, 2018). Emotional contagion from the owner to the dog was recorded by the assessment of the cardiac responses during the Trier social stress test (TSST). Synchronization of the RMSSD levels between the owner and the dog during a stressful condition was found to positively correlate with the duration of the ownership (Katayama et al., 2019). Oxytocin-level correlation was recorded between the owner and the dog during a short-term interaction (Handlin et al., 2012). Owner-dog synchronization of cortisol levels was confirmed during dog agility competition (Jones and Josephs, 2006; Buttner et al., 2015). Furthermore, a recent study showed evidence of long-term synchronization of stress levels between owners and dogs (Sundman et al., 2019). Research on interspecies human-dog chemo-signaling revealed that dogs' behavioral and heart responses were affected by human body odor changes, induced by different emotional states such as happiness and fear (D'Aniello et al., 2018).

CONCLUSION AND FURTHER DIRECTIONS

Our main goal was to review and summarize the current advancement and scattered and dispersed research on positive-emotion in dogs. As previously discussed, prior research has focused on behavioral, cognitive, physiological, endocrine, and neurobiological approaches in dogs' positive-emotion assessment.

Behavioral indicators have been shown to be contradictory and highly context-dependent. Therefore, environmental conditions need to be taken into consideration when interpreting the results. Another major issue with behavioral indicators is the high intra- and interindividual variability in responses (Beerda et al., 1997; Bell et al., 2009; Biro and Adriaenssens, 2013; Goold and Newberry, 2017). One possible solution to these issues could be the implementation of artificial intelligence in behavior analyses. Machine learning and deep learning algorithms could provide useful solutions in detecting subtle differences in behavioral responses caused by different valence and try to find response patterns to a specific positive-emotion eliciting stimulus. But for the moment, behavioral parameters should be used as complementary indicators of emotional valence and supported by other measurements.

Research findings on cerebral asymmetry have identified diverse lateral biases toward qualitatively different emotion stimuli, suggesting the relevance of this asymmetry to animal well-being and welfare research (Rogers, 2010). However, further research on brain lateralization is necessary to deepen our understanding of positive-emotion and emotional information perception, processing, and response in dogs.

Implementing cognitive bias testing is another promising means to assess the emotional responses and overall well-being of a dog (Burman et al., 2011; Kis et al., 2015; Wells et al., 2017). Therefore, more research studies are required in this area. However, the role of temperament traits as a predictor of cognitive bias remains to be further explored (Barnard et al., 2018).

More and more evidence suggests that QBA is a reliable, dynamic qualitative method for positive-emotion and welfare assessment (Stockman et al., 2011; Fleming et al., 2016; Minero et al., 2016, 2018; Collins et al., 2018; Patel et al., 2019). This tool seems to be particularly beneficial in assessing the overall well-being of dogs, for example, in a shelter environment (Walker et al., 2016; Arena et al., 2019).

Certain physiological (e.g., heart rate and superficial temperature) and neurobiological (e.g., amygdala activation) measures are good indicators of arousal; however, they have also been shown to correlate with more than one type of emotional state (Beebe-Center and Stevens, 1937; Kostarczyk and Fonberg, 1982; Garavan et al., 2001; Hamann et al., 2002; Bonnet et al., 2015; Proctor and Carder, 2016; Travain et al., 2016). Again, applying artificial intelligence in data analysis to find specific patterns of responses or changes in time series might prove useful in the identification of qualitative and quantitative differences in positive-emotion processing and responses.

HRV markers have been found to be sensitive to both valence and intensity of emotion (Katayama et al., 2016; Zupan et al., 2016). These promising findings need to be further explored by implementing additional HRV parameters to measure valence and arousal aspects of positive-emotion-eliciting stimuli under well-controlled conditions.

Some of the noninvasive salivary endocrine measures have been validated only recently, and more research is needed in the area. Nevertheless, the common methodological issues in endocrine measures have been identified as subject-related (intra- and interindividual variability), experiment-related (lack of standardization in methodology, impact of sampling time, owner presence, and data interpretation), and context-related (both the impact of testing and regular living environment). Standardized methodology and well-controlled experiments are required to validate endocrine measures as reliable indicators of positive well-being in animals (Cobb et al., 2016; Rault et al., 2017; Chmelíková et al., 2020).

Research evidence shows that both fMRI and fNIRS might be very useful tools in the systematic exploration of positive-emotion processing in dogs. fNIRS and fMRI are comparative methods sensitive to similar physiologic changes. While implementing neuroscientific research into dogs' positive assessment can enhance our knowledge, the fMRI is technically demanding and requires pre-trained animals, which limits studies to small sample sizes. On the other hand, fNIRS is portable, with higher tolerances to motion, and cost-effective; and it requires no restraint of animals. The disadvantage of fNIRS over fMRI is a limited spatial resolution (Scarapicchia et al., 2017).

Furthermore, we have proposed additional psychophysiology approaches which could be complementary to the existing methods in the assessment of both short-term emotional responses as well as longer-term emotional states. Moreover, we would like to stress again the great potential and importance of affective computing in animal emotion research, especially in recognizing subtle differences among emotional responses or by detecting specific patterns in time series of single biosignals or by combining multimodal input data (Caridakis et al., 2007; Yin et al., 2017; Quesnel et al., 2018). For example, deep learning might be particularly helpful in developing a newer methodology for fast detection of regions of interest and accurate, reliable data extraction and analyses in infrared imaging (Marzec et al., 2016; Sonkusare et al., 2019).

Overall, it is too early to conclude whether a certain method or technique in positive-emotion research on dogs is more suitable than others. Prevalent methodological issues and the chronic problem of small sample sizes show that there is a huge need for well-controlled studies with larger numbers of participants. Some approaches show more promising results than others, but the great amount of ambiguous and contrasting findings points toward certain issues that need to be addressed before proceeding further:

a. The relevance of dog temperament in emotion perception, regulation, and responses. Research findings indicate the importance of temperament in dogs' emotion processing and responses (e.g., Cook et al., 2014, 2018; Barnard et al., 2018). Thus, the role of temperament in dog emotion assessment deserves to be investigated further. Implementing validated and reliable dog temperament questionnaires (e.g., PANAS, C-BARQ, MCPQ-R, VIDOPET) (Sheppard and Mills, 2002; Hsu and Serpell, 2003; Ley et al., 2009; Rayment et al., 2016; Turcsán et al., 2018; Savalli et al., 2019) could potentially reduce variability in studies (Manteca and Deag, 1993) and shed additional light on inter-individual differences in dogs' emotion processing and responses.

b. Establishing the reward value prior to testing. Positive-emotion eliciting stimuli used in previous studies are mostly pleasure-related (e.g., hedonic taste, pleasurable touch). However, not all food is automatically *liked* by, and thus pleasure-eliciting for all dogs. The liking aspects depend both on individual preferences and levels of hunger, satiation, or satiety. Despite the fact that owner-dog physical interaction is generally regarded as a positive social reward, not all human interaction might present a positive experience. For example, petting dogs in certain areas might be an unpleasant experience for a dog (Kuhne et al., 2014a). Therefore, close attention needs to be paid to the real value of the reward to a dog. Besides, the arousal aspect of the stimulus should be taken into account as well, since it might affect the response strength. The impact of the testing environment might further complicate the issue, since a novel environment might present a stressor to a dog and thus possibly reduce the hedonic valuation of rewards.

c. Dissecting *wanting* and *liking* components of reward (Berridge et al., 2009). When measuring responses to pleasure eliciting stimuli, researchers should focus separately on each phase of the pleasure cycle (**Figure 1**). As we have previously discussed, distinct reward-related motivational, emotional, and cognitive processes are activated, each with separable neurobiological mechanisms during appetitive, consummatory, and satiety phase (Berridge et al., 2009; Berridge and Kringelbach, 2011). Furthermore, reward delay during the anticipatory phase may lead to frustration (Amsel, 1958).

d. Controlling the impact of dogs' social cognition, attachment, and emotion contagion. The unique psychological characteristics of the owner-dog relationship might significantly impact the measured emotion responses in dogs. Owner-dog relationship or attachment style questionnaires (e.g., MDORS, PAQ) (Dwyer et al., 2006; Zilcha-Mano et al., 2011) could be implemented when dogs are being tested in the presence of the owner, or when owner-dog interaction is used to induce positive-emotion in dogs. Besides, as dogs pay close attention to human emotional signals and cues and act accordingly, this must be taken into consideration during testing conditions as well (Merola et al., 2012; Salamon et al., 2020).

As the research findings show, no single valid method currently exists to reliably assess positive-emotion in dogs. Therefore, great caution is advised when interpreting behavioral, physiological, or endocrine indicators alone (de Vere and Kuczaj, 2016). Multiple noninvasive approaches, combining behavioral, noninvasive physiological, endocrine, and neural measures, need to be implemented to get a rigorous and reliable assessment of qualitative and quantitative differences of emotions in dogs (Paul et al., 2005; Boissy et al., 2007; de Vere and Kuczaj, 2016).

Overall, this review indicates that the research field concerning canine positive-emotion remains largely unexplored, offering researchers opportunities for discoveries that would deepen our knowledge of positive-emotion perception, processing, and recognition, with possible implications for both research and practice to improve the positive well-being and welfare of our companion animals.

AUTHOR CONTRIBUTIONS

EC reviewed the literature and wrote the manuscript. EM reviewed and approved the final manuscript. Both authors contributed to the article and approved the submitted version.

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Wolves and Dogs May Rely on Non-numerical Cues in Quantity Discrimination Tasks When Given the Choice

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A wide array of species throughout the animal kingdom has shown the ability to distinguish between quantities. Aside from being important for optimal foraging decisions, this ability seems to also be of great relevance in group-living animals as it allows them to inform their decisions regarding engagement in between-group conflicts based on the size of competing groups. However, it is often unclear whether these animals rely on numerical information alone to make these decisions or whether they employ other cues that may covary with the differences in quantity. In this study, we used a touch screen paradigm to investigate the quantity discrimination abilities of two closely related group-living species, wolves and dogs, using a simultaneous visual presentation paradigm. Both species were able to successfully distinguish between stimuli of different quantities up to 32 items and ratios up to 0.80, and their results were in accordance with Weber's law (which predicts worse performances at higher ratios). However, our controls showed that both wolves and dogs may have used continuous, non-numerical cues, such as size and shape of the stimuli, in conjunction with the numerical information to solve this task. In line with this possibility, dogs' performance greatly exceeded that which they had shown in other numerical competence paradigms. We discuss the implications these results may have on these species' underlying biases and numerical capabilities, as well as how our paradigm may have affected the animals' ability to solve the task.

Keywords: numerical competence, quantity discrimination, Weber's law, non-numerical information, wolves, dogs

INTRODUCTION

The ability to discriminate different quantities proves to be a very useful tool for humans and animals alike. For example, assessing which areas have the most food and mating opportunities, as well as the fewest predators or competitors, often requires at least basic quantity judgment skills. Therefore, it is not surprising that a large array of species have demonstrated numerical competence to a certain extent ranging from insects (Reznikova and Ryabko, 2011; Gatto and Carlesso, 2019), to cuttlefish (Yang and Chiao, 2016); to vertebrates such as fish (Agrillo et al., 2010; Gómez-Laplaza and Gerlai, 2011; Potrich et al., 2015), amphibians (Krusche et al., 2010; Lucon-Xiccato et al., 2018), lizards (Miletto Petrazzini et al., 2018), tortoises (Gazzola et al., 2018), birds (Hunt et al., 2008; Ditz and Nieder, 2016; Kelly, 2016), and mammals (Hauser et al., 2003; Jordan and Brannon, 2006; Beran et al., 2008; Pisa and Agrillo, 2009; Irie and Hasegawa, 2012; Vonk and Beran, 2012).

Species that live in groups and defend home ranges benefit especially from possessing numerical abilities, as they provide them with useful information to decide whether to engage in inter-group conflict during territory defense (Manson and Wrangham, 1991). In a seminal study, McComb et al. (1994) found that lionesses were less likely to approach an audio playback of three unfamiliar female lions than a playback of a single female and groups of two were less likely to approach the speaker than groups of three or more. This was the first of a number of studies to show that group-living animals are able to assess resource-holding potential (i.e., the ability to acquire or defend resources; Parker, 1974) on the basis of relative group size (e.g., chimpanzees: Wilson et al., 2001; hyenas: Benson-Amram et al., 2011; howler monkeys: Kitchen, 2004; banded mongooses: Furrer et al., 2011; dogs: Bonanni et al., 2010, 2011; and wolves: Harrington and Mech, 1979; Cassidy et al., 2015).

Although such studies provide great insights into the natural behavior of the animals, they are unable to identify the precise mechanisms that the animals utilize to make quantity judgments. For example, it is possible that animals rely on perceptual cues, such as the cumulative size or the density of the stimuli, to assess quantity, rather than using the absolute number of items presented. Experimental studies have therefore endeavored to control for these cues. For example, Jordan and Brannon (2006) used a delayed match-to-sample paradigm whereby rhesus macaques were trained to choose between two options, one of which (the correct choice) contained the same number of items as a previously demonstrated sample stimulus. They systematically tested for the influence of element size, cumulative surface area, and density; they found that monkeys do base their choices on number, regardless of these continuous cues (see also Beran et al., 2008; Hunt et al., 2008; Gross et al., 2009; and Agrillo et al., 2011 for similar examples).

There are several factors that affect an animal's capability to discern between quantities. First and foremost, performance conforms to Weber's law in most species. This law states that the capacity to discriminate between two quantities increases as the ratio between them decreases (i.e., animals should perform better when discriminating between 2 and 8 items –a ratio of 0.25– than between 6 and 8 –a ratio of 0.75; Agrillo and Bisazza, 2014). Other factors that seem to affect performance in numerical tasks are the magnitude (defined as the total amount across both quantities; e.g., the magnitude of 6 vs. 8 would be 14) and the disparity (the absolute difference between the two quantities; e.g., the disparity of 6 vs. 8 would be 2). Thus, as magnitude *increases*, performance *decreases*; and the same happens when disparity *decreases* or the ratio becomes *more even* (Irie and Hasegawa, 2012).

Additionally, these factors seem to compound in such a manner that the effect of the ratio on performance is enhanced when higher magnitudes are presented. Hence, the difference in performance between smaller and larger ratios is less pronounced or even absent when lower numbers are used than when higher ones are (e.g., a high ratio like 0.75 can be discriminated at low magnitudes –such as 3 vs. 4– but not at high ones – like 12 vs. 16). This effect has been found in several species, including guppies (Agrillo et al., 2012), New Zealand robins (Hunt et al., 2008), domestic chicks (Rugani et al., 2008), and humans (Agrillo et al., 2012).

Interestingly, although magnitude does increase the effect of the ratio, absolute upper limits for magnitude do not seem to apply in most cases. As long as the ratio is low enough for them to distinguish, most vertebrates seem to discriminate quantities regardless of the total amount of items present (Agrillo et al., 2010, 2012; Beran and Parrish, 2016).

The effect of ratio and magnitude on performance in numerical tasks has led some researchers to believe that the processing of the different parts of the number range may be regulated by two distinct systems: one that can process only small quantities, but in a precise and fast manner (known as the "object-file" system) and the other that has seemingly no upper limit in magnitude, but is subject to a limit in ratio (known as the analog magnitude system) (Feigenson et al., 2004; Agrillo et al., 2012).

The numerical capabilities of a vast number of species have been tested within different settings and through several distinct paradigms. Two closely related species that have been investigated both under field and lab conditions are wolves and dogs.

Although both wolves and dogs have shown to be able to distinguish between different quantities in intergroup-conflicts under natural conditions (Harrington and Mech, 1979; Bonanni et al., 2010, 2011; Cassidy et al., 2015), their response in controlled lab experiments markedly differs. The first experimental studies in dogs revealed mixed results, with a preferential looking time task finding that dogs can discriminate between 1 vs. 2 and 2 vs. 3 (West and Young, 2002), whereas in a food choice task the dogs seemed unable to distinguish between two amounts of food differing only by one piece, regardless of the ratio (Ward and Smuts, 2007). In a following study using a sequential presentation paradigm where pieces of food were dropped one-by-one into a bowl, the dogs were unsuccessful in all pairings but 1 vs. 0 (Macpherson and Roberts, 2013). However, Macpherson and Roberts (2013) also piloted a paradigm with one dog whereby non-food stimuli were simultaneously presented on two boards, of which the dog could select one. In this setup, the dog was successful on a variety of pairings using numbers from 0 to 9, suggesting factors such as training, presentation of the stimuli, and food visibility may have affected dogs' performance in previous studies.

So far, wolves have shown greater success in quantity discrimination tasks. Utrata et al. (2012) performed a study in which two sets of 1 to 4 pieces of food were inserted sequentially into two opaque tubes. The subjects could then choose one of the tubes, the larger set being considered the correct choice in all cases. The wolves were able to discriminate all pairs and were not affected by ratio (up to 0.75) with these low numbers. Crucially, the study controlled for the potential influence of the amount of time it took to insert different quantities of items. During these controls, the experimenter would insert additional stones into the tube with less food pieces so that the same number of items would be dropped on both sides, and thus they would require approximately the same amount of time to fill.

Wolves also outperformed dogs tested on the exact same paradigm (Range et al., 2014). The dogs were successful only on ratios up to 0.50, which suggests a potential difference between dogs and wolves in numerical competence. These results were reexamined by Miletto Petrazzini and Wynne (2017), who tested wolves and dogs by using the same quantity pairings but with a different method of stimuli presentation; they presented the food items simultaneously on two trays and allowed the animals to choose one of them. Their results corroborate those of Utrata et al. (2012) and Range et al. (2014), with wolves performing above chance on all pairs and dogs showing success only at ratios up to 0.50. Taken together, these studies suggest some differences in numerical discrimination capabilities between wolves and dogs and raise the question of whether they rely on the same information to make their quantity judgments.

The observed differences could come either as a result of the process of domestication, their social ecology, or a combination of both. On one hand, as Frank (1980) hypothesized, the domestication process may have reduced the effect of natural selection on dogs, leaving them with comparatively worse cognitive abilities. On the other, as proposed by Marshall-Pescini et al. (2017), differences in problem solving abilities between wolves and dogs may come as a result of adaptation to the niches they occupy. In this specific case, it is possible that assessing the numbers of competitors in inter-group conflicts is less important for dogs due to their more relaxed social dynamics (Mech and Boitani, 2010; Cafazzo et al., 2014) than wolves, for whom these conflicts inflict the highest natural mortality rate (Smith et al., 2015). Further, the feeding ecology of both species would also conform to this, as both pet and free-ranging dogs usually have easy access to food resources (Vanak and Gompper, 2009; Newsome et al., 2014) while wolves rely on hunting for sustenance and have a considerable probability of failure for each hunting bout (Mech and Boitani, 2010), which again makes quantity discrimination skills more relevant in wolves, as appropriately choosing the larger amount of food (e.g., the larger herds) may be vital for their survival.

All of the above studies are limited in terms of the magnitudes presented, their ability to control for some possibly confounding factors, and their ecological significance. In all these studies, magnitudes were low (with dogs being tested with numbers up to 9 and wolves up to 4), which may dampen the effect of the ratio on the subjects' performance. Testing the animals with bigger numbers would likely not be feasible when using sequential paradigms as that would require them to memorize the quantities of two large sets of items, which could make it harder for them to draw comparisons. Moreover, the numbers used in these experiments may not be reflective of the natural conditions of the animals at least in the context of intergroup conflicts; dogs are facultatively social and usually live solitarily or in small packs, but they are also known to form groups of around 10 individuals; while wolf packs have an average size of around 5–8 individuals, and can go up to 42 (Font, 1987; Daniels and Bekoff, 1989; Bonanni et al., 2010; Cafazzo et al., 2014; Miklosi, 2015). Thus, testing them on numbers up to four may not make sense from a socio-ecological standpoint.

In addition to limited magnitude, the use of different quantities of food as the item to be counted may have been a confounding factor, as the subjects were rewarded even when they chose the smaller amount. Fernand et al. (2018) showed in a reverse-reward contingency task that dogs do not change their choices when selecting a specific stimulus gives them a smaller reward, possibly because they are rewarded regardless of their choice.

Thus, the aim of the current study is to expand on the literature by addressing some of the remaining questions on the topic of canid numerosity. We investigated dogs' and wolves' performance at discriminating quantities presented with different ratios and magnitudes, the latter of which were divided in two phases (with low and high numbers).

Both pet dogs and wolves raised in captivity were tested in this study. They were trained to select either a larger or smaller quantity of dots, presented simultaneously on a touch screen. They were then tested on both familiar (those used during the training) and novel pairs of quantities ranging from 1 to 8. The subjects that showed success in this stage were subsequently tested in a second phase using numbers ranging from 1 to 32. Using a touch screen to assess the quantity discrimination abilities of carnivores has been successfully done in the past (Vonk and Beran, 2012), and touch screens have also been used with canids prior to the current study (Range et al., 2008). Thus, we decided to use a touch screen paradigm, which allowed for greater standardization in the presentation of stimuli, avoidance of potential experimenter cues, removal of the possibly confounding effect of the presence of food during the choice, and the ability to control non-numerical cues in great detail. Thus, unlike in previous studies, the current study controlled for cumulative surface area and spacing and shape of the array of stimuli.

We predicted that dogs would be successful on ratios up to 0.50, but would drop in performance on higher ratios and, in the second stage, higher magnitudes. Furthermore, since the use of continuous cues is often favored over numerical ones (Xiong et al., 2018), we predicted that removing the ability to use the former would result in poorer overall performance when compared with previous studies. Although wolves have not shown a ratio effect to date, Weber's law is predicted to have a greater influence on larger numbers (Lemmon, 1928; Moyer and Landauer, 1967), therefore, we predicted wolves would be successful on all ratios in the first stage and show reduced success on higher magnitudes and ratios in the second stage.

MATERIALS AND METHODS

Experimental Set-Up

Apparatus and General Set-Up

We tested both the dogs and the wolves with a touch screen apparatus donated by Dietmar Schinnerl. It consisted of a flat

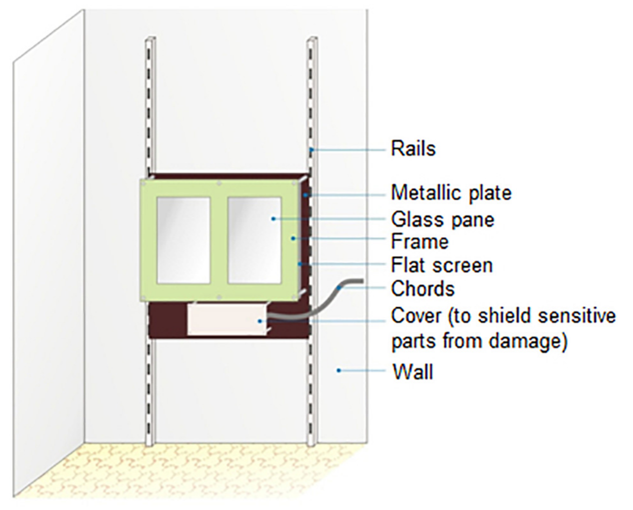

FIGURE 1 | Schematic of the touch-screen used in this study.

screen fixed on a metal plate and mounted on a set of rails (see **Figure 1**); the height of the screen could be individually adjusted by moving the apparatus along the rails. Two separate acrylic glass panes were placed in front of the screen: one covering the left side and the other one the right side. Subjects would make their choices by pressing these glass panes with their muzzle, which activated the pressure-measuring elements to which the panes were connected. These pressure sensors were linked to a computer (which was running the program and recording the subjects' inputs) and to a remote control that triggered a treat dispenser ("Manners Minder" by Premier), which would emit a high-pitched noise and release a treat in rewarded trials if the choice was correct (more information about the different types of trials below).

Stimuli Used

The stimuli were created and presented with an application written in "C#" (by Dietmar Schinnerl), based on ".NET Framework 2.0." The stimuli consisted of randomized arrangements of different numbers of black dots on a white background. Stimuli pairs were divided between the ones with "small" numbers (1–8 dots in each stimulus) and those with "large" numbers (8–32 dots in each stimulus)[1]. The combinations of small and large numbers had similar ratios to each other except for one of the pairs presented to the dogs in which, due to an error, the combination of 16 vs. 32 dots (with a ratio of 0.50) was displayed instead as 16 vs. 22 dots (ratio of 0.73) for all but one of the tested subjects. A detailed account of all combinations throughout the training and test phases can be found in **Table 1**.

Every stimulus had a constant cumulative surface area (black area) always covering 20% of each side of the screen (thus, cumulative surface area remained constant between the two stimuli of every single pair). Conversely, both dot sizes and positions were randomly chosen with the specification that all dots had a diameter of at least 0.5 cm. Stimuli were presented semi-randomly, with the smaller combination of dots being shown on the left side in half of the trials and on the right side the other half. Some examples of stimulus combinations are provided in **Figure 2**.

Stevens et al. (2007) proposed that stimulus density (i.e., if the dots are arranged in a clustered or spread manner) could also act as a confounding factor when measuring the ability to discriminate between quantities. Because of this, in trials where the stimulus pair included a single dot (the "one" stimulus), the dots on the other side were clustered (a combination of stimuli we named "One/Cumulated"). Since the position of the dots in all other pairs were pseudo-randomized (in such a manner that none of the dots came in contact with one another), the density between the stimuli was comparable for these other combinations.

Another possible influencing factor would be that the animals made their choice based on simple perceptual rules, such as picking the side with the biggest dot or avoiding the one with the smallest dot. Thus, in half of the trials without a "one," the side that had the biggest dot was counterbalanced (half of the time on the larger quantity stimulus, half of the time on the smaller quantity stimulus; we named this combination "Biggest dot/Random") and in the other half of the trials without a "one," the smallest dot was counterbalanced in the same way ("Smallest dot/Random").

General Procedure and Experimental Conditions

Ethics Statement

No special permission for use of animals (wolves and dogs) in such socio-cognitive studies is required in Austria (Tierversuchsgesetz 2012–TVG 2012). The relevant committee that allows running research without special permissions regarding animals is: Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria).

General Procedure

In each trial, the subjects were presented with a pair of stimuli, each displayed on each side of the touch screen. These stimuli showed different amounts of dots. Depending on the group they were assigned to, subjects were trained to press the side with the larger amount (group 1) or the side with the smaller one (group 2).

If the subjects made a correct choice, the screen turned white for 1 second, a high-pitched tone would play from the reward dispenser, and a reward would be released. If the choice was incorrect, the screen turned red for 5 s, the computer connected to the touch screen played a lower-pitched tone, and no reward was given. If the animals made an incorrect choice, the trial would be repeated until the subject made the correct choice. The subjects were not restricted, and could freely move toward the touch screen and back at any point during the trials.

Each session consisted of around 30 trials (27–35 depending on the condition and level, see below) plus correction trials. Trials

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[1] The number 8 was used mostly on "small" number pairs, but one pair of "large" numbers does contain it (namely, 8:24; see **Table 1**). This was due to the relative lack of number pairs with low ratios within the large numbers group.

TABLE 1 | Number pairs used in all phases, with their respective ratios.

Phase 1

Training pairs									
Pairs	1:8	1:7	1:6	1:5	1:4	2:8	2:7	2:6	3:8
Ratios	0.13	0.14	0.17	0.20	0.25	0.25	0.29	0.33	0.38

Probe pairs

Level	**Pairs**				**Ratios**			
1	1:3	2:5	4:8		0.33	0.40	0.50	
2	3:7	1:2	3:6	4:6	0.43	0.50	0.50	0.67
3	2:4	3:5	5:7		0.50	0.60	0.71	
4	4:7	2:3	5:6		0.57	0.66	0.83	
5	5:8	3:4	6:7		0.63	0.75	0.86	
6	6:8	4:5	7:8		0.75	0.80	0.88	

Phase 2

Training pairs									
Pairs	1:8	1:4	9:32	2:6	9:27	8:24	3:8	11:29	12:31
Ratios	0.13	0.25	0.28	0.33	0.33	0.33	0.38	0.38	0.38

Probe pairs

Level	**Pairs**				**Ratios**			
7	10:30	12:30	9:18		0.33	0.40	0.50	
8	12:28	11:22	16:32[†]	14:21	0.43	0.50	0.50[†]	0.67
9	13:26	15:25	17:24		0.50	0.60	0.71	
10	18:32	19:29	15:18		0.56	0.66	0.83	
11	10:16	21:28	19:22		0.63	0.75	0.86	
12	24:32	12:15	22:25		0.75	0.80	0.88	

Trained pairs were used for rewarded trials in both the training and the test phase. Novel pairs were used only in the probe trials of the test sessions (with each level having its own set of novel pairs). [†]For all but one of the dogs, the 16:32 pair of numbers (with a ratio of 0.5) was not presented by mistake. Instead, the 16:22 (ratio of 0.73) was used. All wolves were tested with the 16:32 pair.

were organized in two phases: phase 1 (in which only "small" numbers were presented) and phase 2 (where "large" numbers were introduced). A training phase would take place before each testing phase. In these training phases, the subjects were trained to discern between different pairs of numbers (shown in **Table 1**). These "training" pairs from each training phase would then be presented in the subsequent testing phase but they were always rewarded if the choice was correct.

Rewarded trials were interspersed with unannounced "probe" trials to test the numerical competence of the animals. In these probe trials, novel pairs of numbers were presented and no feedback was given (i.e., the screen turned black for 1 s, no tone was played, and no reward was given). The absence of feedback precluded any possibility of learning, since we presented these combinations of quantities more than once. Sessions never started –nor ended– with unrewarded trials; at least 3 rewarded trials were presented in a row before the first unrewarded trial and after the last one.

Each testing phase consisted of 6 levels with 4 sessions each. Levels increased in difficulty by presenting number pairs of increasing ratios in the probe trials (see **Table 1**).

After the subjects finished either the first or the second testing phase, they were subjected to a control phase, with new stimuli designed to control for any possible non-numerical cues they may have used.

Training Phase 1

Training sessions were comprised of 31 trials. In these trials, number pairs with small ratios (up to 0.38) were presented in a randomized sequence (see **Table 1**), with each pair being shown 3 or 4 times per session.

In four random trials in each session, the outcome was the same as in probe trials (i.e., neither feedback nor a reward was given). This was done to prepare the subjects for the probe trials in test sessions, so that they would be accustomed to getting no feedback for some trials.

The criterion to reach the next phase was to reach at least 80% accuracy at first choice in two consecutive sessions on two different days.

Phase 1 (Levels 1–6)

Test sessions were divided in six levels of four sessions each. In these sessions, there were 27 rewarded trials in which the number

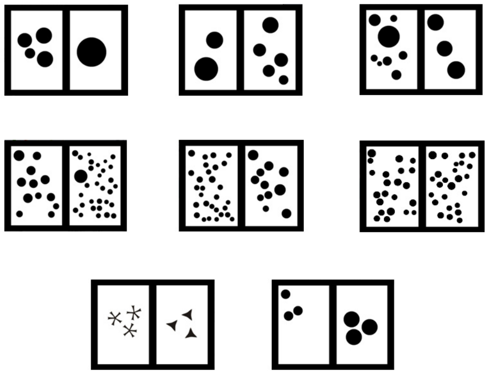

FIGURE 2 | Examples of different stimuli combinations. **(Top row)** "small" numbers: from left to right; 4 vs. 1 (One/Cumulated combination), 2 vs. 5 (Biggest dot/Random combination, largest dot on the left –the lower number), and 8 vs. 3 (Smallest dot/Random, smallest dot on the left –the higher number). **(Middle row)** "large" numbers: from left to right; 12 vs. 31 (Biggest dot/Random, largest dot on the right –the higher number), 29 vs. 11 (Biggest dot/Random, largest dot on the right –the lower number), and 22 vs. 25 (Smallest dot/Random, smallest dot on the right –the lower number). **(Bottom row)** control stimuli: left: combination used for shape control trials, right: combination used for size control trials.

pairs shown in the training phase were presented (nine different pairs, repeated three times), as well as six (or eight) probe trials; (3 different pairs, repeated twice, 4 in the case of level 2), with new pairs of numbers. In total, each session was composed of 33 trials (or 35 in level 2).

For the dogs, the configuration of the program was changed after starting the experiment. Initially, it was made so that no more than two probe trials were presented in a row. However, when five dogs already performed on the first levels (Toffee: level 4, Ida: level 2, Miley: level 4, Xela: level 4, and Guinness: level 3), we observed that some of them made more mistakes in the trial following a probe trial (usually by pressing again the same side – or promptly changing sides– without noticing the new stimuli), so we discarded all probe trials that took place after another probe trial and excluded them from any analyses. We then changed the configuration so that a probe trial was always followed by a rewarded trial to avoid this effect. All wolves, as well as all other dogs, were tested with the new configuration.

Training for Phase 2

This training phase was similar to the first with the exception that no practice probe trials were presented (thus reducing the amount of trials to 27 per session), and that some larger quantities (but still with ratios up to 0.38) were introduced (see **Table 1** for details). This time, the criterion to pass to the next phase was at least 85% of correct first choices in two consecutive sessions on two different days. Additionally, it was necessary to make fewer than three wrong first choices on the new larger pairs of stimuli in each of those sessions.

Phase 2 (Levels 7–12)

Phase 2 was similar to phase 1 but, once again, some mistakes did take place in the sessions carried out by the wolves. The combinations used in this phase's probe trials had larger numbers but they were otherwise designed to match as much as possible the ratio of those in the first phase (**Table 1**).

Control Sessions

To further control for the use of non-numerical cues, a final set of six control sessions was run. In these sessions, the rewarded trials were akin to those of the first training phase, but probe trials presented new pairs of stimuli in order to control for the influence of dot size and overall shape of the stimulus. Thus, probe trials in this phase were divided in two types: size control trials and shape control trials. For the size control, we presented the same number of dots on both sides, but they were larger on one side than on the other (in order to check if they used average dot size instead of the number of dots to make their choice; see **Figure 2**). For the shape control, we showed the subjects another combination of stimuli with the same number and cumulative surface area on both sides but one of the sides had star-like shapes instead of dots, while the other had triangle-like shapes [these two shapes were meant to emulate the appearance of the negative space (white area) between the arrays of large or small amounts of dots; as an asterisk-like form or a triangular-like one, respectively; see **Figure 2**].

These control sessions were comprised of 27 rewarded trials and six control trials (three for each kind of control), making a total of 33 trials. Overall, every type of control was presented 18 times per subject (21 times in case of some wolves).

Statistical Analyses

Analyses were conducted with R 3.6.1 (R Core Team, 2019). Performance above chance was tested by using exact binomial tests, comparing the different subsets of the data with a probability of success of 0.5. We also ran generalized mixed models [GLMM; "glmer" function "lme4" package, Bates et al. (2015)] with a binomial distribution and a logit link function, two for each phase of the experiment (one for rewarded trials and one for probe trials). For control trials, models were made for each type of control trial (shape control and size control); and probability of choosing one of the options over the other was analyzed, again, with exact binomial tests. Due to the differences in testing, raising, and housing conditions, all analyses were made separately for dogs and wolves.

The response variable in all models was the first choice of each trial (either "correct" or "wrong"). The rest of the fixed variables and interactions were selected partly based on the Akaike Information Criteria. The "individual" was added as a random effect. Random slopes structure was set with the help of a function devised by Roger Mundry, who also wrote the function we used to check for overdispersion. Models were analyzed with Wald χ^2 tests ("car" package; Fox and Weisberg, 2018) to detect effects.

As the stimulus that was presented in the correct side was a nested variable of the pair of stimuli presented, *post hoc* Wilcoxon tests were used to compare the probability of success for both of the stimuli within each pair (adjusting the *p*-value according to the Holm method for multiple comparisons).

Due to the results of control sessions, an additional *post hoc* model was run to assess the potential use of non-numerical cues by some of the dogs (more details in the results section). Graphs were created through the ggplot2 (Wickham, 2016), sjPlot (Lüdecke, 2018b), and sjmisc (Lüdecke, 2018a) packages.

STUDY 1: DOGS

Subjects

Thirty-one pet dogs aged 1–9 years were recruited from an existing pool of subjects and their owners at the Clever Dog Lab, Vienna. Eleven of these dogs (two of them with previous touch screen experience and nine of them without it) dropped out during the pre-training phase due to lack of motivation, leaving a final sample size of $n = 20$, with an average age of 4.51 ± 2.62 years. Dogs were assigned semi-randomly to the two experimental groups. Sex (6–8 females and 3 males per group), and age (on average 4.60 ± 2.86 years for group 1 and 4.43 ± 2.41 for group 2) were counterbalanced as much as possible. Dogs from various breeds were tested (see **Supplementary Table 1** in the **Supplementary Material** for further details) and were as well matched to the extent possible between the groups.

Testing Facility and Set-Up

The study took place in a 2.9 m × 3.5 m room of the Clever Dog Lab in Vienna. At the first appointment the dogs had time to familiarize themselves with the room and the experimenter, to feel comfortable in the situation. Training and testing sessions took place once or twice per week for about 30–60 min each. For shaping and rewarding, positive reinforcement was used exclusively (further details about the pre-training are provided in the **Supplementary Material**).

The touch screen used for the dogs had a resolution of 1024 pixels × 748 pixels, and the glass panes in front of it were 13.5 cm × 22 cm each. The distance between screen and dispenser was 2.5–2.8 m, to ensure the animals moved away from the screen and therefore observed the new stimuli before making a choice in the next trial. For three dogs (Bertl, Chilly, and Flora) the distance was reduced by half due to them approaching the dispenser slower than the rest of the subjects. To avoid any unintentional cues given by the owner or the experimenter, a plywood panel was fixed next to the screen. Both the owner and experimenter remained behind this panel from the first training phase onwards.

Results

Training Phase 1

Out of the 20 dogs trained, two of them (Shiloh and Flora) did not achieve the testing criterion and dropped out of the experiment. Another two dogs (Chilly and Havanna) completed this training phase but did not continue with the rest of the experiment. The remaining 16 dogs continued with the phase 1 of the study.

The dogs that completed the training session required a varying amount of trials to achieve the learning criterion, averaging at 626.47 ± 335.58.

Test Phase 1

Training trials

The performance on the trials after a probe trial varied significantly from the other rewarded trials (GLMM: z = 6.110, $p < 0.001$). Thus, these trials were excluded from further analyses.

Performance was above chance on the remaining rewarded trials (binomial test: probability of success = 0.908, C.I. 95%: 0.901–0.914, $p < 0.001$). Furthermore, dogs chose the correct side above chance for every single combination of numbers (see **Table 2**). Probability of success was also above chance for every combination of stimuli (binomial test; biggest circle/random: probability of success = 0.829, C.I. 95%: 0.811–0.846, $p < 0.001$; smallest circle/random: probability of success = 0.903, C.I. 95%: 0.889–0.917, $p < 0.001$; one/cumulated: probability of success = 0.941, C.I. 95%: 0.934–0.948, $p < 0.001$).

Factors affecting the performance of the animals. Despite the fact that the animals performed above chance on every number pair (**Table 2**) as well as each of the combinations used to control for perceptual features, success was dependent on ratio (decreasing as the ratio increased, see **Figure 3**; Wald $\chi^2 = 39.860$, $p < 0.001$) and the combination of stimuli (Wald $\chi^2 = 29.769$, $p < 0.001$). The combination that controlled for the side with the biggest dot yielded the lowest amount of correct choices (biggest dot/random vs. smallest dot/random: $z = 2.167$, $p = 0.030$; biggest dot/random vs. one/cumulated: $z = 4.680$, $p < 0.001$). When further analyzing performance within each combination of stimuli, we only found significant differences in the biggest dot/random trials, with fewer correct choices when the stimulus with the biggest dot was not the correct one (Wilcoxon: $W = 428744$, $p < 0.001$). We found no such differences in the other combination of stimuli (Wilcoxon: smallest dot/random: $W = 392486$, $p = 1$; one/cumulated: $W = 2424752$, $p = 1$). This suggests that dogs used the size of the dots presented to make their choices, picking the side with the largest dot significantly more than the other stimulus.

We also found a learning effect (Wald $\chi^2 = 16.5484$, $p = 0.005$), with the performance of every level aside for the second being significantly better than the first one (GLMM: level 1 vs. 2:

TABLE 2 | Probabilities of success for the pairs of numbers presented in rewarded trials in the first phase of study 1 (dogs).

Ratio	Numbers presented	Probability of success	95% confidence interval		*p*=
0.13	1:8	0.976	0.964	0.985	<0.001
0.14	1:7	0.970	0.957	0.980	<0.001
0.17	1:6	0.942	0.924	0.956	<0.001
0.20	1:5	0.926	0.906	0.942	<0.001
0.25	1:4	0.893	0.871	0.912	<0.001
0.25	2:8	0.894	0.872	0.914	<0.001
0.29	2:7	0.867	0.843	0.889	<0.001
0.33	2:6	0.858	0.834	0.881	<0.001
0.38	3:8	0.845	0.820	0.868	<0.001

Probability of success calculated with exact binomial tests, comparing performances with a 0.5 probability of success by chance. Rows with the same background color indicate number pairs with the same ratio.

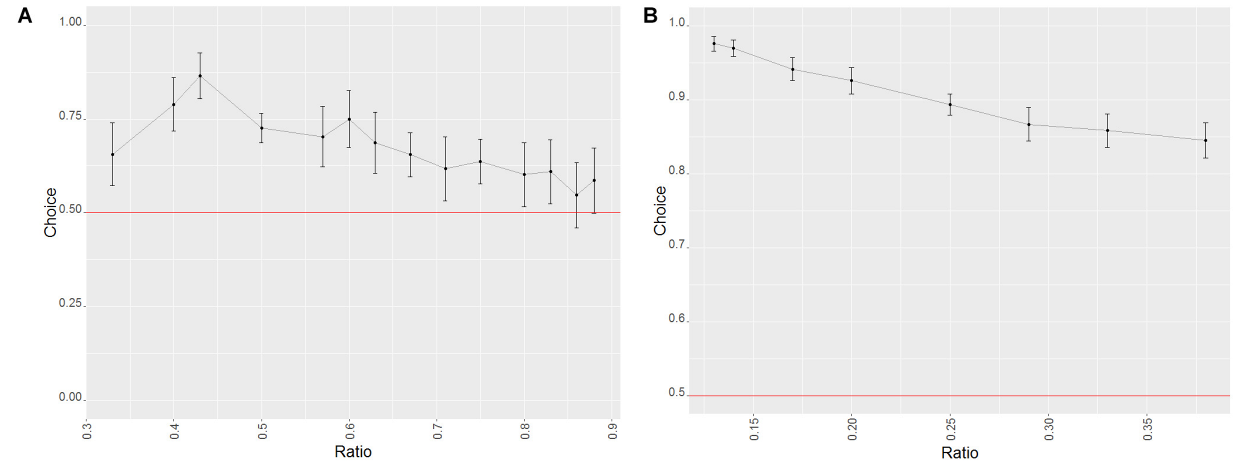

FIGURE 3 | Effect of the ratio on the probability of success in trials of phase 1 of study 1 (dogs). Error bars set at the 95% confidence interval; the red line represents probability of success by chance. **(A)** Probe trials. **(B)** Training trials.

z = 1.208, p = 0.227; level 1 vs. 3: z = 1.985, p = 0.047; level 1 vs. 4: z = 2.292, p = 0.022; level 1 vs. 5: z = 3.489, $p < 0.001$; level 1 vs. 6:z = 2.854, p = 0.004). An effect of group was also found, but there were no significant differences between the groups (Wald χ^2 = 4.780, p = 0.029; GLMM: group 1 vs. group 2 z = −1.413, p = 0.157).

Test (probe) trials

Dogs performed above chance on probe trials (binomial test: probability of success = 0.677, C.I. 95%: 0.657–0.696, $p < 0.001$). Performance was above chance for all number pairs except for 6:7 and 7:8 (see **Table 3**) and in all combinations of stimuli (binomial test; biggest dot/random: probability of success = 0.662, C.I. 95%: 0.632–0.690, $p < 0.001$; smallest dot/random: probability of success = 0.702, C.I. 95%: 0.673–0.729, $p < 0.001$; one/cumulated: probability of success = 0.638, C.I. 95%: 0.575–0.698, $p < 0.001$).

Factors affecting the performance of the animals. Success in probe trials was influenced by the ratio (with higher ratios yielding worse performances, see **Figure 3**; Wald χ^2 = 47.334, $p < 0.001$) as well as the combination of stimuli presented (Wald χ^2 = 14.552, $p < 0.001$), although no difference between the three combinations was found (GLMM: biggest dot/random vs. one/cumulated: z = −1.212, p = 0.226; biggest dot/random vs. smallest dot/random: z = 1.028, p = 0.304). When taking into consideration only biggest dot/random trials, dogs were more successful when the side with the biggest dot was the correct one (Wilcoxon: W = 151528, p = 0.003), which again suggested that dogs used the size of the dots at least to some degree to make their decisions. We found no such differences in any of the other combinations of stimuli (Wilcoxon: smallest dot/random: W = 140156, p = 1; one/cumulated: W = 8258, p = 0.259).

Training Phase 2

Only eight dogs out of the 16 that completed the previous test phase were trained for the second phase of the study (although all of them did participate in the control phase later on). Three of those subjects (Ida, Oszkar, and Miley) did not complete this training phase, leaving a total of five dogs that continued toward phase 2 of the experiment. The dogs that completed the second training phase required an average of 873.00 ± 690.91 trials to do so.

TABLE 3 | Probabilities of success for the different number pairs presented in probe trials in the first phase of study 1 (dogs).

Ratio	Numbers presented	Probability of success	95% confidence interval		p=
0.33	1:3	0.656	0.566	0.739	<0.001
0.40	2:5	0.784	0.702	0.853	<0.001
0.43	3:7	0.873	0.799	0.927	<0.001
0.50	1:2	0.620	0.527	0.707	0.011
0.50	2:4	0.754	0.668	0.828	<0.001
0.50	3:6	0.760	0.674	0.833	<0.001
0.50	4:8	0.788	0.703	0.858	<0.001
0.57	4:7	0.698	0.610	0.777	<0.001
0.60	3:5	0.752	0.665	0.826	<0.001
0.63	5:8	0.688	0.600	0.766	<0.001
0.67	2:3	0.628	0.536	0.714	0.006
0.67	4:6	0.675	0.583	0.758	<0.001
0.71	5:7	0.610	0.518	0.696	0.019
0.75	3:4	0.641	0.551	0.723	0.002
0.75	6:8	0.633	0.543	0.716	0.003
0.80	4:5	0.602	0.511	0.687	0.027
0.83	5:6	0.603	0.512	0.689	0.026
0.86	**6:7**	**0.547**	**0.457**	**0.635**	**0.331**
0.88	**7:8**	**0.586**	**0.496**	**0.672**	**0.063**

Probability of success calculated with exact binomial tests, again a 0.5 probability of success by chance. Number pairs with the same ratio are shown with the same background color. Rows with numbers in bold indicate that success was not above chance level for that pair of numbers.

Phase 2

Training trials

As was the case in Phase 1, there was a significant variation in performance on trials after a probe trial (GLMM: $z = 4.360$, $p < 0.001$). Therefore, those trials were excluded from any further analyses.

Dogs correctly chose the respective stimuli above chance in the rewarded trials of the second phase (binomial test: probability of success = 0.849, C.I. 95%: 0.834–0.863, $p < 0.001$), and the same applied to every pair of numbers (see **Table 4**). Performance was also above chance for every combination of stimuli (binomial test; biggest circle/random: probability of success = 0.806, C.I. 95%: 0.779–0.831, $p < 0.001$; smallest circle/random: probability of success = 0.889, C.I. 95%: 0.867–0.908, $p < 0.001$; random/cumulated: probability of success = 0.852, C.I. 95%: 0.820–0.881, $p < 0.001$).

Factors affecting the performance of the animals. As was the case for the rewarded trials of phase 1, success decreased as the ratio increased (Wald $\chi^2 = 21.681$, $p < 0.001$; see **Figure 4**) and the combination of stimuli influenced performance with the combination biggest dot/random yielding worse performances than both smallest dot/random, and one/cumulated (Wald $\chi^2 = 24.093$, $p < 0.001$; GLMM: $z = 1.981$, $p = 0.048$; $z = 3.797$, $p < 0.001$). Within the different combinations of stimuli, once again, we found differences only in the combination that controlled for side of the biggest dot, with worse performances when the side with the largest dot wasn't the correct one (Wilcoxon: $W = 121173$, $p < 0.001$). No differences were found in the other stimulus combinations (Wilcoxon: small dot/random: $W = 123683$, $p = 1$; one/cumulated: $W = 36949$, $p = 1$).

Test (probe) trials

Overall probe trials in the second phase were performed above chance level (binomial test: probability of success = 0.730, C.I. 95%: 0.697–0.762, $p < 0.001$). All pairs of numbers representing a ratio below 0.63 were selected above chance. Above that, only 14:21, 17:24, 21:28, and 12:15 were successfully discriminated (see **Table 5**). Probability of success remained above chance for both combinations of stimuli (binomial test; biggest dot/random: probability of success = 0.695, C.I. 95%: 0.646–0.741, $p < 0.001$; smallest dot/random: probability of success = 0.765, C.I. 95%: 0.720–0.808, $p < 0.001$; since none of the number pairs contained a "one" stimulus, the "one/cumulated" combination was not present in these trials).

TABLE 4 | Probabilities of success for the ratios and number pairs presented in rewarded trials in the second phase of study 1 (dogs).

Ratio	Numbers presented	Probability of success	95% confidence interval		p=
0.13	1:8	0.967	0.938	0.985	<0.001
0.25	1:4	0.741	0.685	0.792	<0.001
0.28	9:32	0.861	0.815	0.900	<0.001
0.33	2:6	0.792	0.740	0.838	<0.001
0.33	9:27	0.849	0.801	0.890	<0.001
0.33	8:24	0.884	0.840	0.919	<0.001
0.38	3:8	0.830	0.781	0.873	<0.001
0.38	11:29	0.857	0.810	0.896	<0.001
0.38	12:31	0.835	0.786	0.876	<0.001

Probability of success calculated with exact binomial tests, comparing performances with a 0.5 probability of success by chance. Rows with the same background color indicate pairs of numbers with the same ratio.

Factors affecting the performance of the animals. For the test trials in this phase, only the ratio (Wald $\chi^2 = 7.568$, $p = 0.006$) had a significant effect (with a decrease in success the higher the ratio; see **Figure 4**), as the effect of the stimulus combination was non-significant (Wald $\chi^2 = 2.721$, $p = 0.099$). This seems to imply that the dogs' overall bias toward the side with the largest dot was absent in probe trials for the second phase.

Control Phase

All dogs that completed at least one of the test phases –except for Oszkar and Guinness– participated later on the control phase, leaving a sample size of 14 for this phase of the study.

Shape control

Dogs chose the side with triangular shapes over the one with stars (binomial test: probability of choosing triangles = 0.676, C.I. 95%: 0.613–0.735, $p < 0.001$). Furthermore, the individuals from group 2 (the ones trained to choose the smaller number of dots) chose triangles significantly more than the other group (GLMM: $z = 4.265$; $p < 0.001$). However, individuals from group 1 did not show this preference for the triangular shape (binomial test: probability of choosing triangles = 0.484, C.I. 95%: 0.394–0.575, $p = 0.789$).

Size control

Our subjects chose the side with the largest dots over the one with the smallest ones (binomial test: probability of choosing bigger dots = 0.770, C.I. 95%: 0.711–0.822, $p < 0.001$). As with the shape control, the group that was trained for fewer dots chose larger dots significantly more than the other group (GLMM: $z = 4.525$, $p < 0.001$). However, in this case, the group trained for the bigger amount did also choose the larger dots above chance (binomial test: probability of choosing bigger dots = 0.627, C.I. 95%: 0.536–0.711, $p = 0.006$).

Post hoc Average Size Control

Due to the results of the control phase and the detailed analyses of the various experimental phases, we ran a final model to assess the performance of both groups in only the trials with the number combinations with the most similar inter-stimulus dot size: the pairs differing in just one number (i.e., 1:2, 2:3, 3:4, 4:5, 5:6, 6:7, and 7:8).

There was no significant effect of group in these trials, nor of the interaction between group and the pair of stimuli (Wald $\chi^2 = 0.077$, $p = 0.781$; Wald $\chi^2 = 0.054$, $p = 0.973$; respectively). As stated above, dogs performed above chance level in all number pairs except for 6:7 and 7:8.

However, we also did not find any effect from any of the variables used in other models (including ratio: Wald $\chi^2 = 2.498$, $p = 0.114$; see **Supplementary Figure 1**).

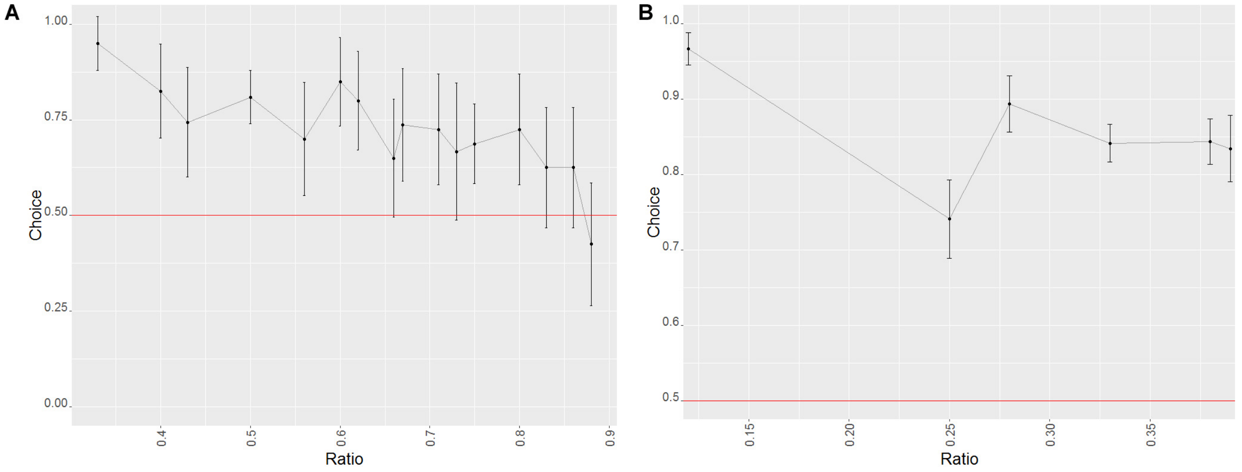

FIGURE 4 | Effect of the ratio on the probability of success in the trials of phase 2 of study 1 (dogs). Error bars set at the 95% confidence interval; the red line represents probability of success by chance. **(A)** Probe trials. **(B)** Training trials.

Discussion for Study 1

Our data suggest that pet dogs are able to distinguish between two numbers, and that their performance in these quantity discrimination tasks decreases as the ratio increases (as predicted by Weber's law). Nonetheless, continuous variables (such as dot size) seem to have influenced the performance of our subjects throughout the study. Contrary to both the results of previous studies and our own predictions, dogs were able to distinguish ratios higher than 0.50. More than that, in phase 1, they succeeded in almost every single combination for which they had received no training and they still had a good rate of success on the combinations with higher magnitudes in phase 2.

There are several possibilities that may explain this higher level of performance. One of them is that the use of the touch screen removes the confounding effect of the presence of food. In other studies, food was given to the dogs whether or not they made the correct choice, which made even wrong choices not very costly. Fernand et al. (2018) found a similar effect in a reverse-reward contingency task, in which the dogs kept choosing the larger stimulus, even though the outcome of that choice would leave them with a smaller reward.

Also to be taken into consideration is the relative difficulty of this task when compared to the sequential procedure we previously used (see Range et al., 2014). The sequential paradigm required the subjects to keep in mind both quantities before drawing comparisons, a process that may have been too cognitively demanding. Conversely, the subjects were able to perceive both stimuli at the same time in this study, which may have facilitated their choices, thus improving their performance. Nonetheless, Miletto Petrazzini and Wynne (2017) presented both stimuli simultaneously and their results seem to match those of the sequential task, so other factors may be at play as well such as the extensive training phase.

Previous studies focused on spontaneous choices (toward the highest quantity of food items), while we exposed our subjects to extensive training to induce them to choose either the highest or lowest amount of items. Some authors have drawn attention to the possibility that giving animals extensive training to perform a quantity discrimination task may re-purpose neuro-cognitive systems that are normally not concerned with

TABLE 5 | Probabilities of success for the different ratios and pairs of numbers presented in probe trials in the second phase of study 1 (dogs).

Ratio	Numbers presented	Probability of success	95% confidence interval		*p*=
0.33	10:30	0.950	0.831	0.994	<0.001
0.40	12:30	0.825	0.672	0.927	<0.001
0.43	12:28	0.744	0.579	0.870	0.003
0.50	9:18	0.850	0.702	0.943	<0.001
0.50	11:22	0.763	0.598	0.886	0.002
0.50	13:26	0.800	0.644	0.909	<0.001
0.57	18:32	0.700	0.535	0.834	0.017
0.60	15:25	0.850	0.702	0.943	<0.001
0.63	10:16	0.800	0.644	0.909	<0.001
0.67	**19:29**	**0.650**	**0.483**	**0.794**	**0.080**
0.67	14:21	0.737	0.569	0.866	0.005
0.71	17:24	0.725	0.561	0.854	0.006
0.73	**16:22**†	**0.667**	**0.472**	**0.827**	**0.099**
0.75	21:28	0.725	0.561	0.854	0.006
0.75	**24:32**	**0.650**	**0.483**	**0.794**	**0.081**
0.80	12:15	0.725	0.561	0.854	0.006
0.83	**15:18**	**0.625**	**0.458**	**0.773**	**0.154**
0.86	**19:22**	**0.625**	**0.458**	**0.773**	**0.154**
0.88	**22:25**	**0.425**	**0.270**	**0.591**	**0,430**

Probability of success calculated by using exact binomial tests, comparing the subjects' performances with a 0.5 probability of success by chance. Pairs of numbers with the same ratio share a background color in the table. Numbers in bold indicate that the probability of success for that number pair was not above chance. †The 16:22 pair of numbers was mistakenly presented instead of the intended one (16:32) for all but one of the dogs. As only one of the subjects was tested for the correct pair, we didn't analyze its probability of success.

numerical competence, so it is certainly possible that our training may have not only taught the subjects "which stimulus to choose" but also "how to choose better in general" (Barnard et al., 2013; see Agrillo and Bisazza, 2014 for a detailed comparison between the spontaneous and trained approaches). In guppies, for example, extensive training has been shown to increase numerical competence skills (Bisazza et al., 2014). Accordingly, our extensive training might have directed their attention to the relevant features of the task (quantity) making it easier to successfully choose between the harder pairs of stimuli that they were not trained for (Zentall and Riley, 2000). Further research with both spontaneous choice and training procedure paradigms should be done to further explore the mechanisms behind this difference in performance.

In any case, the procedure used seems to have an influence on the outcome of quantity discrimination tasks in dogs. This is not an isolated case, as angelfish show a higher upper limit of ratio when tested to choose the highest amount of food than when approaching the biggest shoal (Gómez-Laplaza and Gerlai, 2011; Gómez-Laplaza et al., 2018). Just as Gómez-Laplaza et al. (2018) discussed, differences in motivation (in this case, only receiving a reward with correct choices) and cognitive abilities required by the task (perceiving both numbers at once instead of having to remember them) may have driven the contrast between our results and those found previously in the literature.

STUDY 2: WOLVES

Subjects

Eleven wolves participated on this study, with ages averaging 3.77 ± 1.08 years. All of the wolves had previous touch-screen experience (see **Supplementary Table 2** in the **Supplementary Material** for further details).

All of the wolves were hand-raised with conspecifics in peer groups, after being separated from their mothers in the first 10 days after birth. They were bottle-fed and later hand-fed by humans and had continuous human interaction in the first 5 months of their lives. After that, they were introduced into packs with other adult wolves and currently live in large 2,000–8,000 m^2 enclosures.

The wolves were tested in a 2.6 m × 3 m room at the Wolf Science Center in Ernstbrunn, Austria. All subjects were familiarized with the room prior to the sessions (usually ranging between 10 and 45 min) and were, overall, conducted with less regularity compared to the dogs; sessions usually took place only once a week except for breeding season (when some animals would refuse to work) or when other tests were carried out. A maximum of one session per day was carried out for every subject.

As was the case for the dogs, the wolves were divided into two groups (with group 1 being trained to choose big numbers, and group 2 to choose small numbers). Further, like the dogs, we counterbalanced the groups by sex (3 males and 2 or 3 females per group) and age (3.96 ± 0.67 years for group 1 and 3.61 ± 1.32 years for group 2).

Whenever testing was interrupted for a long period of time, the subjects would have to repeat the respective training phase until they achieved once again the learning criterion.

Testing Facility and Set-Up

The touch screen used for the wolves was similar to that used for the dogs, with a few differences in size (the glass panes having a size of 20 cm × 26 cm, and the resolution of the screen being 1,920 pixels × 1,080 pixels). Since the treat dispenser did not work well with the food rewards used for the wolves (mixture of dry food and meat), the experimenter would reward the subjects when their choices were correct and, instead of the dispenser playing a sound, the experimenter would use the sound of a clicker as a reinforcer. To avoid any possible experimenter cues, the experimenter stood on the side opposite to the touch screen, next to the dispenser (which made it impossible for the subjects to look at the experimenter at the same time they were making a choice), and was otherwise instructed to maintain a neutral facial expression during the trials. The distance between the treat dispenser and the touch screen was the same as that used for the dogs. No plywood panel was placed next to the screen for this experiment.

Stimuli and procedures for the wolves were identical as the ones used for the dogs.

Results

Training for Phase 1

Two of the wolves that were trained for this task (Geronimo and Yukon) did not achieve the testing criterion and were subsequently excluded from the experiment. The remaining nine wolves completed the training phase in an average of 486.86 ± 426.77 trials. Due to problems during the data management process, the records for the training trials of two of the subjects (Aragorn and Shima) were lost, and thus are not included in this analysis.

Phase 1

Some of the sessions in this phase (the last two sessions of level 4 for Una, the first two sessions of level 5 for Aragorn, and the first two sessions of level 4 as well as the entirety of level 3 for Amarok) were lost during the data management process, and thus are not included in any of the analyses. Furthermore, due to human error, some individuals received more than four sessions per level, but these additional sessions were not included in any analysis either.

Eight of the nine individuals tested in this phase completed all 6 levels; Una was eventually dropped (after she completed level 5) due to lack of motivation.

Training trials

Performance on trials after a probe trial differed significantly from the rest of the rewarded trials (GLMM: $z = 4.192$, $p < 0.001$), and as such, they were excluded.

Performance was above chance on training trials (binomial test: probability of success = 0.873, C.I. 95%: 0.863–0.883, $p < 0.001$), and every number combination used was correctly selected above chance level as well (see **Table 6**). Probability of success was also above chance for all three combinations

TABLE 6 | Probabilities of success for the pairs of numbers presented in rewarded trials in the first phase of study 2 (wolves).

Ratio	Numbers presented	Probability of success	95% confidence interval		p=
0.13	1:8	0.957	0.934	0.974	<0.001
0.14	1:7	0.950	0.925	0.968	<0.001
0.17	1:6	0.911	0.882	0.936	<0.001
0.20	1:5	0.907	0.878	0.932	<0.001
0.25	1:4	0.854	0.819	0.885	<0.001
0.25	2:8	0.838	0.800	0.871	<0.001
0.29	2:7	0.825	0.787	0.858	<0.001
0.33	2:6	0.801	0.763	0.836	<0.001
0.38	3:8	0.820	0.781	0.854	<0.001

Probability of success calculated with exact binomial tests, comparing performances with a 0.5 probability of success by chance. Rows with the same background color indicate number pairs with the same ratio.

of stimuli (binomial test; biggest circle/random: probability of success = 0.757, C.I. 95%: 0.728–0.784, $p < 0.001$; smallest circle/random: probability of success = 0.886, C.I. 95%: 0.864–0.906, $p < 0.001$; one/cumulated: probability of success = 0.916, C.I. 95%: 0.903–0.927, $p < 0.001$).

Factors affecting the performance of the animals. Even though all number pairs were correctly chosen above chance level, success was still affected by ratio (with a lower amount of successful choices the higher the ratio; Wald $\chi^2 = 14.566$, $p < 0.001$, see **Figure 5**) and combination of stimuli (with the biggest dot/random combination yielding significantly worse results than the one/cumulated combination: Wald $\chi^2 = 36.887$, $p < 0.001$; GLMM: $z = 0.756$, $p < 0.001$). Furthermore, we did find a significant difference in performance within the biggest dot/random trials, with overall fewer correct choices when the side with the largest dot was not the correct one (Wilcoxon: $W = 428744$, $p < 0.001$), which does suggest that our subjects may have been using this stimulus as a non-numerical cue to inform their choices. No differences were found between the stimuli of the smallest dot/random and one/cumulated combinations (Wilcoxon: $W = 105088$, $p = 1$, Wilcoxon: $W = 676750$, $p = 1$; respectively).

Test (probe) trials

Performance on unrewarded probe trials was above chance level (binomial test: probability of success = 0.644, C.I. 95%: 0.618–0.671, $p < 0.001$), and the same remained true for every combination of stimuli (binomial test; biggest circle/random: probability of success = 0.619, C.I. 95%: 0.576–0.660, $p < 0.001$; smallest circle/random: probability of success = 0.658, C.I. 95%: 0.618–0.696, $p < 0.001$; one/cumulated: probability of success = 0.685, C.I. 95%: 0.602–0.760, $p < 0.001$). Most number pairs up to a ratio of 0.80 were successfully discriminated by the subjects (except for 2:3, 5:7; and 6:8; see **Table 7**).

Factors affecting the performance of the animals. Only the ratio had an effect in probe trials (Wald $\chi^2 = 10.038$, $p = 0.002$; see **Figure 5**), with no perceived differences between the different combination of stimuli (Wald $\chi^2 = 1.574$, $p = 0.455$), suggesting a reduced use of non-numerical information in probe trials when compared to the number pairs that the subjects were trained for.

Training for Phase 2

Six out of the eight wolves that completed phase one went through the training for phase 2. The average number of trials they needed to proceed to the test phase was of 2702.00 ± 2092.97.

Phase 2

A sizable amount of the records for the sessions in this phase were lost due to complications in the data management process (the entirety of levels 2, 3, 4, and 5 for Chitto, as well as the two last sessions of level 1 and the first of level 6; levels 5 and 6 for both Nanuk and Shima; level 2 and the first session of level 3 for Aragorn; and the last session of level 4 for Kaspar). These sessions were thus not included in any of the analyses.

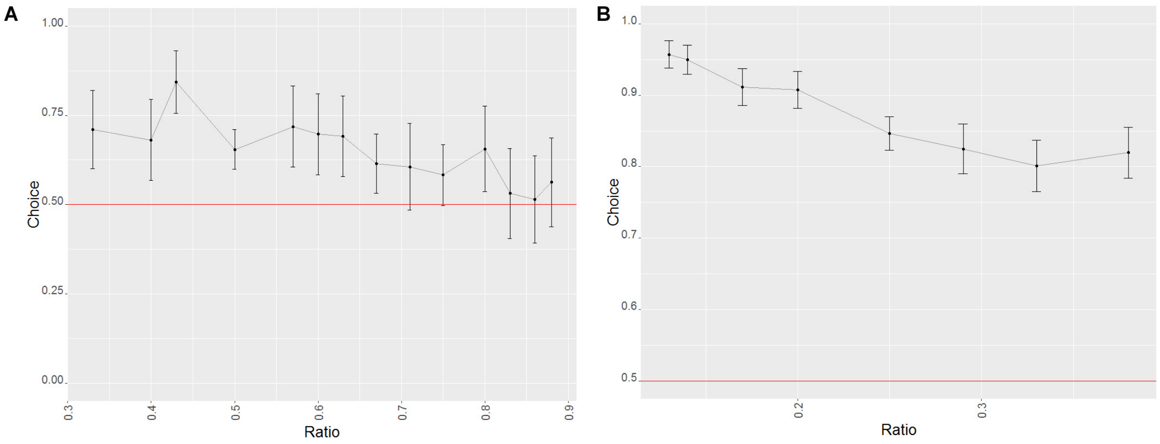

FIGURE 5 | Effect of the ratio on the probability of success in the trials of phase 1 of study 2 (wolves). Error bars set at the 95% confidence interval; the red line represents probability of success by chance. **(A)** Probe trials. **(B)** Training trials.

TABLE 7 | Probabilities of success for the different number pairs presented in probe trials in the first phase of study 2 (wolves).

Ratio	Numbers presented	Probability of success	95% confidence interval		*p*=
0.33	1:3	0.710	0.588	0.813	<0.001
0.40	2:5	0.681	0.558	0.788	0.003
0.43	3:7	0.843	0.736	0.919	<0.001
0.50	1:2	0.648	0.525	0.758	0.017
0.50	2:4	0.682	0.556	0.791	0.004
0.50	3:6	0.662	0.540	0.770	0.009
0.50	4:8	0.629	0.505	0.741	0.041
0.57	4:7	0.718	0.592	0.824	<0.001
0.60	3:5	0.697	0.571	0.804	0.002
0.63	5:8	0.691	0.567	0.798	0.002
0.67	**2:3**	**0.594**	**0.464**	**0.715**	**0.169**
0.67	4:6	0.634	0.511	0.745	0.032
0.71	**5:7**	**0.606**	**0.478**	**0.724**	**0.109**
0.75	3:4	0.632	0.507	0.746	0.038
0.75	**6:8**	**0.531**	**0.402**	**0.657**	**0.708**
0.80	4:5	0.656	0.527	0.771	0.017
0.83	**5:6**	**0.531**	**0.402**	**0.657**	**0.708**
0.86	**6:7**	**0.515**	**0.390**	**0.638**	**0.904**
0.88	**7:8**	**0.563**	**0.433**	**0.686**	**0.382**

Probability of success calculated with exact binomial tests, again a 0.5 probability of success by chance. Number pairs with the same ratio are shown with the same background color. Rows with numbers in bold indicate that success was not above chance level for that pair of numbers.

Furthermore, as with the first phase of the experiment, some individuals received additional sessions after their fourth for some of the levels due to human error. Once more, these trials were excluded from analyses.

Training trials

We found the performance of rewarded trials to be significantly different when the trials after a probe trial were taken into consideration (GLMM: $z = 4.192$, $p < 0.001$), so those trials were excluded from any further analyses.

Probability of success remained above chance level for the training trials of this phase (binomial test: probability of success = 0.829, C.I. 95%: 0.812–0.844, $p < 0.001$), and so did the probability of success for every combination of stimuli (binomial test; biggest circle/random: probability of success = 0.752, C.I. 95%: 0.720–0.781, $p < 0.001$; smallest circle/random: probability of success = 0.854, C.I. 95%: 0.828–0.876, $p < 0.001$; one/cumulated: probability of success = 0.913, C.I. 95%: 0.884–0.936, $p < 0.001$). All number pairs were successfully discerned above chance levels (see **Table 8**).

Factors affecting the performance of the animals. Similarly to the training trials in phase 1, we found an effect both of the ratio (Wald $\chi^2 = 14.066$, $p < 0.001$; see **Figure 6**) and the combination of stimuli, with a significant difference between the biggest dot/random and the one/cumulated combinations (Wald $\chi^2 = 17.443$, $p < 0.001$; GLMM: $z = 2.148$, $p = 0.032$) on this type of trials in phase 2. We also found a decrease in successful trials whenever the side with the biggest dot was not the correct one within the biggest dot/random combination of stimuli (Wilcoxon: $W = 87546$, $p = 0.023$), indicating, once again, a possible use of the side with the largest dot as a non-numerical cue to solve the task. No such effects were found for the other combinations of stimuli (smallest dot/random: Wilcoxon: $W = 93489$, $p = 1$; one/cumulated: Wilcoxon: $W = 28251$, $p = 1$).

TABLE 8 | Probabilities of success for the pairs of numbers presented in rewarded trials in the second phase of study 2 (wolves).

Ratio	Numbers presented	Probability of success	95% confidence interval		*p*=
0.13	1:8	0.967	0.935	0.985	<0.001
0.25	1:4	0.858	0.808	0.900	<0.001
0.28	9:32	0.796	0.739	0.845	<0.001
0.33	2:6	0.805	0.749	0.854	<0.001
0.33	9:27	0.839	0.788	0.883	<0.001
0.33	8:24	0.821	0.766	0.867	<0.001
0.38	3:8	0.794	0.736	0.844	<0.001
0.38	11:29	0.751	0.692	0.804	<0.001
0.38	12:31	0.804	0.748	0.853	<0.001

Probability of success calculated with exact binomial tests, comparing performances with a 0.5 probability of success by chance. Rows with the same background color indicate number pairs with the same ratio.

Test (probe) trials

Success in probe trials was overall above chance level (binomial test: probability of success = 0.642, C.I. 95%: 0.604–0.679, $p < 0.001$), which was also the case for both combinations of stimuli (binomial test; biggest dot/random: probability of success = 0.634, C.I. 95%: 0.582–0.684, $p < 0.001$; smallest dot/random: probability of success = 0.651, C.I. 95%: 0.594–0.705, $p < 0.001$; the "one/cumulated" combination was not present in these trials). Regardless, only six number pairs (10:30, 12:30, 9:18, 13:26, 15:25, and 19:29) were discriminated above chance levels (see **Table 9**).

Factors affecting the performance of the animals. As with the probe trials in phase 1, ratio was the only factor that had any bearing on performance (Wald $\chi^2 = 22.474$, $p < 0.001$; see **Figure 6**), as we found no effect of the combination of stimuli (Wald $\chi^2 = 0.286$, $p = 0.5932$).

Control Phase

All of the wolves that participated on the second phase of the experiment were also subjected to the control sessions. However, the records from one of these wolves (Shima) were lost due to problems in data management, and thus not included for any of the analyses.

Shape control

We did find an overall preference toward the "triangle" shape for individuals of both groups (binomial test: probability of choosing triangle = 0.822, C.I. 95%: 0.727–0.895, $p < 0.001$). Furthermore, individuals from group 2 (trained to choose the smaller amount) chose this shape significantly more often than subjects from group 1 (GLMM: $z = 2.963$, $p = 0.003$).

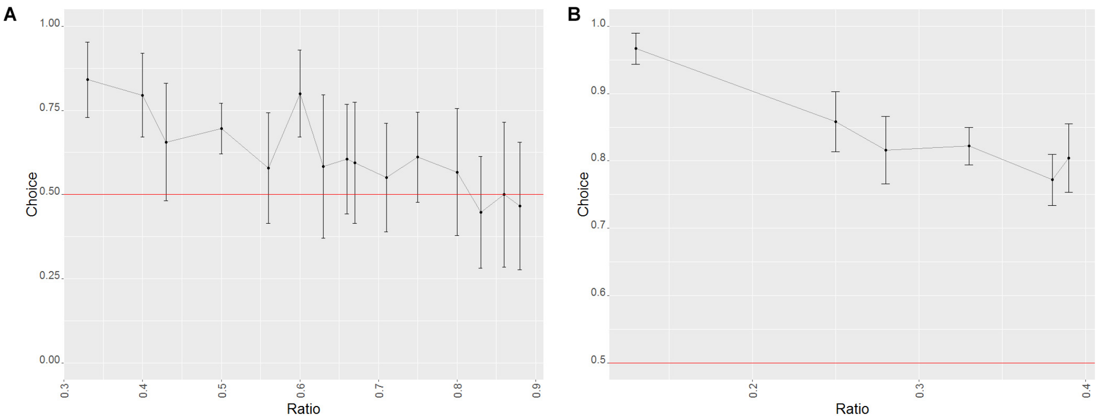

FIGURE 6 | Effect of the ratio on the probability of success in the trials of phase 2 of study 2 (wolves). Error bars set at the 95% confidence interval; the red line represents probability of success by chance. **(A)** Probe trials. **(B)** Training trials.

After further inspection, we found that the individuals from group 2 chose the triangular shape above chance levels (binomial test: probability of choosing triangle = 0.926, C.I. 95%: 0.821–0.979, $p < 0.001$), but those in group 1 did not (binomial test: probability of choosing triangle = 0.667, C.I. 95%: 0.490–0.814, $p = 0.065$).

Size control

When subjects from both groups were taken into account, we did not find any preference toward any of the sizes of the dots (binomial test: probability of choosing the larger dots = 0.444, C.I. 95%: 0.340–0.553, $p = 0.343$). However, we did find an effect of group in our model, with subjects from group 2 showing a preference for the larger dots (GLMM: $z = 1.997$, $p = 0.046$).

After further examination, we observed that the individuals from group 1 chose the stimulus with the smaller dots above chance (binomial test: probability of choosing the larger dots = 0.306, C.I. 95%: 0.163–0.481, $p = 0.029$) and that group 2 has done the same with the stimulus with the larger dots (binomial test: probability of choosing the larger dots = 0.722, C.I. 95%: 0.585–0.835, $p = 0.001$).

TABLE 9 | Probabilities of success for the different ratios and pairs of numbers presented in probe trials in the second phase of study 2 (wolves).

Ratio	Numbers presented	Probability of success	95% confidence interval		p=
0.33	10:30	0.840	0.699	0.934	<0.001
0.40	12:30	0.795	0.647	0.902	<0.001
0.43	**12:28**	**0.656**	**0.468**	**0.814**	**0.110**
0.50	9:18	0.682	0.524	0.814	0.023
0.50	**11:22**	**0.594**	**0.406**	**0.763**	**0.377**
0.50	13:26	0.800	0.644	0.909	<0.001
0.50	**16:32**	**0.686**	**0.500**	**0.839**	**0.0501**
0.57	**18:32**	**0.579**	**0.408**	**0.737**	**0.418**
0.60	15:25	0.800	0.644	0.909	<0.001
0.63	**10:16**	**0.583**	**0.366**	**0.779**	**0.541**
0.67	19:29	0.605	0.434	0.760	0.255
0.67	**14:21**	**0.594**	**0.406**	**0.763**	**0.377**
0.71	**17:24**	**0.550**	**0.384**	**0.707**	**0.636**
0.75	**21:28**	**0.542**	**0.328**	**0.744**	**0.839**
0.75	**24:32**	**0.667**	**0.472**	**0.827**	**0.099**
0.80	**12:15**	**0.566**	**0.374**	**0.745**	**0.585**
0.83	**15:18**	**0.447**	**0.286**	**0.617**	**0.627**
0.86	**19:22**	**0.500**	**0.291**	**0.709**	**1.000**
0.88	**22:25**	**0.467**	**0.283**	**0.657**	**0.856**

Probability of success calculated by using exact binomial tests, comparing the subjects' performances with a 0.5 probability of success by chance. Pairs of numbers with the same ratio share a background color in the table. Numbers in bold indicate that the probability of success for that number pair was not above chance.

Post hoc Average Size Control

To test the implications of the results of the control trials on the wolves' use of non-numerical cues, we once again ran another model with the data from the combinations differing only in one number (as they would have the least differences in overall dot size between stimuli).

We found an effect from the interaction between ratio and group, with the individuals from group 1 showing better performances in trials with higher ratios, as opposed to group 2 (Wald $\chi^2 = 8.067$, $p = 0.005$; see **Supplementary Figure 2** in the **Supplementary Material**). No further effects were found (including ratio: Wald $\chi^2 = 0.531$, $p = 0.466$; see **Supplementary Figure 3** in the **Supplementary Material**).

Out of the number pairs used in this model, some of them (1:2, 3:4, and 4:5) were performed above chance, while the others (2:3, 5:6, and 7:8) were not, as stated above (see **Table 7**).

Discussion for Study 2

In line with the available literature, we found that wolves are able to distinguish between quantities of increasing ratios. Both Utrata et al. (2012) and Miletto Petrazzini and Wynne (2017) showed that wolves are able to discern between quantities differing in ratios up to 0.75, comparable to the maximum of 0.80 that our subjects were able to distinguish above chance in the current study.

We did find, however, an effect of ratio on our subjects' performance with worse performance at higher ratios, in accordance with Weber's law, something that these previous studies did not show. This suggests that the limited numbers used on those paradigms (a maximum of four items to count) may not have been enough to find any difference in performance for different ratios (due to either a ceiling effect or the lack of enough pairs of numbers to find any pattern from their performances). However, it could tentatively provide support as well for the object-file system, which postulates that "low" quantities are processed in a faster, more accurate fashion than "higher" ones (usually up to a maximum of four; Feigenson et al., 2004; Agrillo et al., 2012). Nevertheless, our wolves were not able to distinguish between the stimuli in the 2:3 pair, which would go against this system's predictions as both numbers are low, and yet they were unable to differentiate them above chance.

As expected, the overall results in phase 2 (where higher numbers were used) were considerably worse than those of phase 1 (as fewer number pairs were chosen correctly above chance levels, even though their ratios were comparable to those presented during phase 1). However, due to the very limited data availability for this part of the experiment, we cannot draw any conclusions from this sample.

Finally, we need to draw attention to the fact that several subjects carried out additional sessions in some of the levels due to human error (see **Supplementary Table 3** for more details). Although unlikely, given that the number pairs used in probe trials were exclusive to each level, it remains a possibility that the additional trials may have somehow affected the wolves' performance in the test trials. In contrast, training trials could certainly have been affected by this. However, since we did not find any effect of the level on the probability of success on training trials –in other words, no learning effect– the additional sessions are unlikely to have affected the performance.

GENERAL DISCUSSION

As expected, we found an effect of ratio for both of our species, in accordance with Weber's Law. Dogs were able to discern combinations they were not trained for with ratios up to 0.83 in phase 1, and up to 0.80 in phase 2 (although performance did decrease after 0.63; some combinations above this ratio were discerned correctly above chance while others were not). Wolves, on the other hand, correctly distinguished number pairs with a ratio of up to 0.80 in phase 1, and up to 0.60 in phase 2 (with some pairs with lower ratios not being correctly distinguished in both phases). The seemingly worse results in phase 2 for both species seem to imply that there may also be an effect of magnitude at play, which we had predicted.

We did not study, however, the possibility that a separation between two distinct number processing systems (the object-file system and the analog magnitude system) does take place in canids. According to some authors, the discrimination of quantities up to four is regulated by the object-file system (Feigenson et al., 2004; Agrillo et al., 2012), and those above that number are the domain of the analog magnitude system. In the current study, however, we aimed at testing the subject species at overall high magnitudes, so we decided to make the split between the "high" and "low" numbers at eight, as it provided us with more possible number pairs with the same ratios between both phases of the experiment. Future studies should focus on looking for evidence of presence or absence of both of these systems in dogs and wolves, as well as finding the upper limit for the object-file system if its presence is indeed confirmed.

It remains unclear why some of the combinations were not distinguished when some others with higher ratios were, especially in phase 2 for both of our species. Since this effect seems to be more pronounced in wolves (both being the species with the least amount of individuals tested and the one with a noticeably incomplete dataset), and these fluctuations being present only in phase 2 for dogs (with a drastically reduced amount of individuals), we presume this outcome to be a consequence of the reduced sample size. Still, this difference may have also been partly influenced by the combined effect of ratio and magnitude, with both species failing to distinguish above chance some of the pairs with the highest magnitudes (e.g., 19:29 and 24:32). Future studies should focus on the performance of these species when distinguishing pairs of high magnitudes.

It is worth noting that wolves seem to have performed worse than dogs overall, with fewer number pairs correctly chosen above chance, which could indicate that the wolves were not as focused on the task as the dogs. Wolves' sessions were generally shorter than dogs' (ranging from 10 to 45 min in wolves and 30–60 in dogs), so it is possible that they made their decisions faster, which could have led to an overall higher amount of incorrect choices. Additionally, it is likely that the pet dogs were more at ease within the testing room due to their different upbringing (as they would generally spend more time indoors than the wolves), which could have negatively impacted their concentration.

It is also possible that the less frequent sessions when compared with the dogs (with some individuals participating in this experiment for several years, see **Supplementary Table 2** for more details) may have also negatively influenced the wolves' learning of the skill. Indeed, wolves needed on average 2702.00 ± 2092.97 trials to achieve learning criterion for the second phase of the study, while dogs did it in 873.00 ± 690.91 trials. In general, however, it is important to keep in mind that the wolves and dogs tested here were not comparable in terms of life and experimental experiences, which is why we refrain from drawing direct comparisons here and would also like to caution the against arriving at unwarranted conclusions.

It is up for debate, however, how much of these differences in performance may have come as an actual variation of cognitive abilities and not as merely an artifact of our lacking dataset. Whatever the case, future studies should assess this possible difference in quantity discrimination abilities, especially when higher numbers are used. Were wolves to be less capable than dogs to distinguish quantities when higher numbers are used, it would put in jeopardy the conclusions from previous studies that compared numerical competence between dogs and wolves.

Nonetheless, it appears that both species may have used non-numerical cues in conjunction with the numerical information to solve this task. For instance, both groups in both species seemed to have had a clear preference for the side with the biggest dot, and a higher probability of failure when that was not the correct side. This bias was not prevalent in all trials, however, having a lesser impact in probe trials (especially for wolves, which did not show the bias in these trials). Nevertheless, this effect may have been strong enough to dampen the influence of the ratio, with generally fewer differences in performance per ratio in trials that controlled for the side with the biggest dot (see the **Supplementary Material**). It's possible that our individuals found the larger dot to be a more conspicuous stimulus, and thus had a tendency toward selecting that over the other stimulus with random sizes. Studies in different species have found similar biases toward choosing the largest stimulus, and it has been suggested that this bias may be adaptative in the wild, as choosing the largest pieces of food does usually provide the animal with the most amount of food (Boysen et al., 2001; Beran et al., 2008) although this pattern has not been found in dogs (Miletto Petrazzini and Wynne, 2016). However, given the uneven manifestation of this bias across the conditions and species, it appears to be an artifact of the current setting rather than a phenomenon with real ecological significance. Further research with different paradigms would be needed to determine which of the two possibilities does apply in this case.

More importantly, however, the group trained to choose the smallest amount did select the side with the largest dots and the one with the shapes meant to emulate the negative space between the large dots significantly more often in the control phase, which would be consistent with them choosing based on the appearance of the stimuli rather than the number of dots. That is to say, as the total area covered by the dots had to remain constant between both stimuli, it could be that dogs in group 2 were consistently choosing the side with the biggest dots on average as a rule of thumb to select the side with the lowest number of dots. In dogs, the opposite pattern was not present in group 1 (as the individuals from this group did not choose the star-like shape over the triangular one, nor the smaller dots over the large ones) but wolves trained to select the stimulus with the largest amount of dots did select the stimulus with the smallest ones in the control trials, which would provide credence to them picking the side with the smallest dots regardless of any numerical information. However, since we did not present the two shape control stimuli to the subjects before training them to solve the quantity discrimination task, it remains unclear whether spontaneous preference toward any of the stimuli played a role in their choices, and if it did, to which degree.

Nevertheless, in dogs, the performance of both groups was the same in trials with pairs differing in just one number (the ones with less variation in the average area of the dots between the stimuli). This would imply that, although individuals in group 2 did use alternative cues to solve the task, they also relied on numerical data when that information was not clear enough.

In wolves, however, we did find an effect of the interaction between ratio and group in these trials, with individuals from group 1 performing better at higher ratios than at lower ones (see **Supplementary Figure 2** in the **Supplementary Material**). This does seem to imply that wolves from the first group relied more heavily on non-numerical cues (maybe even exclusively), as their performance was somewhat altered when those cues were not as readily available.

Interestingly, there is no apparent effect of the ratio for these trials with combinations differing on just one number for either of the species. Ward and Smuts (2007) also found a different performance in dogs whenever pairs differing on just one number (i.e., a disparity of one) were presented to the subjects (as they were not able to make the correct choice regardless of the ratio), so it is possible that the low disparity of the numbers used may have dampened the effect of the ratio on the subjects' success. Future studies should look further into the influence of this factor in quantity discrimination tasks.

The fact that the group trained to choose the smallest amount seemed to rely more on non-numerical information (especially in the case of dogs) could be related to the results of other studies about pattern discrimination in animals. In most studies in which two groups of animals are trained to select different options depending on their magnitude (be it quantity, odor intensity, auditory intensity, etc.), the group trained to choose the higher magnitude seems to have an easier time acquiring the skill (Zielinski and Jakubowska, 1977; Pelz et al., 1997; Watanabe, 1998; Vonk and Beran, 2012; see Inman and Pearce, 2018 for a review).

All in all, it seems like the size of the dots may have played an important role in directing the dogs' and wolves' choices. Studies have shown that other species such as fish (Agrillo et al., 2008; Xiong et al., 2018), salamanders (Krusche et al., 2010), cats (Pisa and Agrillo, 2009), and monkeys (Stevens et al., 2007) use mainly non-numerical cues when available, so it should come as no surprise that at least some of our subjects used continuous cues as an aid to solve the task as well (regardless of our efforts in limiting their presence). This could point toward quantity discrimination being an overall more demanding cognitive ability, driving animals to use alternative cues if at all present.

These studies have shown that, although both dogs and wolves are able to distinguish quantities of different ratios and magnitudes, they have a preference toward using non-numerical cues when available. Future studies on canid numerosity should control for non-numerical information more thoroughly (e.g., by having a variable cumulated surface area: making all items presented have the same size on both stimuli in some trials and alternating the side with highest cumulated surface area in others). Furthermore, it would also be interesting to pinpoint, which perceptual cues (density, convex hull, surface area...) allow the animals to make approximations of quantity, and whether they use that information alone in the wild or there is some *sensu stricto* quantity discrimination involved.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because no special permission for use of animals (wolves and dogs) in such socio-cognitive studies is required in Austria (Tierversuchsgesetz 2012–TVG 2012). The relevant committee that allows running research without special permissions regarding animals is: Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria). For all domesticated subjects used, written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

FR acquired the funding. FR and I-MP designed the study. I-MP and MH conducted the experiments. DR-B and RD managed the data. DR-B, MH, and FR took care of the data analysis and its interpretation. The manuscript was written by DR-B, I-MP, and RD, and revised by FR. All authors read and approved the contents of this 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.2020.573317/full#supplementary-material

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BRIEF RESEARCH REPORT
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Human Face Recognition in Horses: Data in Favor of a Holistic Process

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Recent studies have demonstrated that horses can recognize humans based simply on visual information. However, none of these studies have investigated whether this involves the recognition of the face itself, or simply identifying people from non-complex external clues, such as hair color. To go beyond this we wanted to know whether certain features of the face were indispensable for this recognition (e.g., colors, hair or eyes). The 11 horses in this study had previously learned to identify four unfamiliar faces (portrait view and in color) presented repeatedly on a screen. We thus assessed whether they were able to identify these same faces spontaneously when they were presented in four other conditions: profile view, black and white, eyes hidden, changed hairstyle. The horses' performances remained higher than chance level for all the conditions. In a choice test under real conditions, they then approached the people whose face they had learned more often than unknown people. In conclusion, when considering all the individuals studied, no single facial element that we tested appears to be essential for recognition, suggesting holistic processing in face recognition. That means horses do not base their recognition solely on an easy clue such as hair color. They can also link faces from photographs with people in real life, indicating that horses do not process images of faces as simple abstract shapes.

Keywords: face recognition, *Equus caballus*, animal cognition, human–animal relationship, horse model

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INTRODUCTION

Facial recognition capacities have been increasingly studied in animals. They have focused on within- species recognition (pigeons: Nakamura et al., 2003; sheep: Ferreira et al., 2004; capuchins: Pokorny and de Waal, 2009; cattle: Coulon et al., 2011; macaques: Schell et al., 2011) and also of human faces (dogs: Huber et al., 2013; sheep: Knolle et al., 2017; dogs: Mongillo et al., 2017; bees: Avargues-Weber et al., 2018). Similarly, the horse appears to be able to recognize individuals and process faces. Studies have shown it capable of cross-modal recognition of its conspecifics (Proops et al., 2009). Horses can also express emotions through characteristic facial expressions (Dalla Costa et al., 2014; Gleerup et al., 2015; Hintze et al., 2016; Lansade et al., 2018; Trindade et al., 2020) and are able to differentiate these expressions (Wathan et al., 2016). Other studies have demonstrated that horses can identify human beings. For example, they can associate a voice with the sight of a specific person (Lampe and Andre, 2012; Proops and McComb, 2012). Similarly, they can link a facial expression depicting an emotion (joy or anger) with the corresponding vocalization (Nakamura et al., 2018; Trösch et al., 2019). Moreover, horses are capable of identifying in real life a person they had previously only seen in a photograph or video, and of adapting their behavior according to the facial expression or behavior that person had demonstrated (Smith et al., 2016; Proops et al., 2018; Trösch et al., 2020).

Two other studies focused on recognition of human faces. The first, conducted on four horses showed that they could learn to differentiate between two faces and then transfer that facial recognition during a field trial by passing more time with the person whose photograph had been associated with a reward (Stone, 2010). The second demonstrated that horses can both learn to differentiate faces of unknown people from a photograph and also spontaneously identify the photograph of a person they had encountered in real-life, despite not having seen that person for 6 months (Lansade et al., 2020). However, none of these studies has investigated whether this involves the recognition of the face itself, or simply identifying people from non-complex external clues, such as hair color.

This study thus aimed to determine whether horses based their recognition on a single, salient element, possibly even external to the face such as the hairstyle, or on more holistic face processing.

We tested horses which had previously been trained to identify four faces (the "recurrent faces") from photographs presented repeatedly (portrait views, in color). During the tests, we presented the horses with the same recurrent faces under four different conditions: profile, in black and white, with eyes hidden and changed hairstyles. We chose to mask the eyes and the hair with accessories (sunglasses and a wig) rather than masking them a posteriori, so that the portraits remained more realistic, and were less disturbing for the animals. We hypothesized that if horses' recognition ability was based only on a single clue (e.g., eyes) their performances would not differ from chance level under the conditions in which this clue was modified. Finally, to ensure that horses made the link between faces learned on a screen and people in real life and thus did not process facial images as simple abstract shapes, we conducted a choice test with real people (people whose faces had been presented repeatedly vs. totally unknown people).

MATERIALS AND METHODS

Subjects

The study was conducted on 11 3-year-old female Welsh breed horses, bred at the Animal Physiology Experimental Unit PAO, INRA (DOI: 10.15454/1.5573896321728955E12). They were kept in a group at pasture or in a large stall with straw bedding. They had free access to fodder and water. From birth, they had been handled daily by a team of around 15 people (mucking out the stables, distributing food, walking in hand and carrying out basic health care such as clipping hooves, vaccinations, etc.).

Set Up and Previous Training to Touch the Recurrent Faces

The animals were tested individually in a testing area (6 m × 4 m) equipped with a video camera (**Figure 1**). A system consisting of a tactile screen (1.02 m × 0.57 m) linked to a computer with an automatic pellet distributor was located at the end of the area. Horses were led into the area and let loose in front of the system (see Lansade et al., 2020). For the previous training, and the sessions performed for this experiment, horses were individually tested in daily sessions of 32 trials, conducted between 9:00 and 17:00. Each trial began with a blank screen. After 30 s, two photographs appeared simultaneously on the screen. When the horses touched one of them with their nose or did nothing for 30 s the screen became blank again. A reward (5 g of pellets) fell automatically into a feeding trough located just below the screen, according to the conditions described below (training trials or test trials).

Prior to the present experiment, the horses had been trained to touch a "recurrent face" (among 4, Caucasian women, all unknown to the horse in real life) presented on a screen opposite a systematically different novel face to obtain pellets. The four recurrent faces became familiar over successive trials. Each of these "recurrent faces" was presented eight times per training session in a semi-randomized order (one "recurrent face" was never presented more than twice consecutively). Several intermediary steps were conducted to reach this objective (initially, one of the four recurrent faces was presented opposite a black circle, and then opposite novel objects and finally opposite novel faces). The horses learned to complete each step successfully (75% of correct responses on two consecutive sessions) within 2–5 sessions respectively, see Lansade et al. (2020) for more details.

The images of the recurrent and control faces were digital photographs taken by ourselves with a NIKON D3300. The photographs of novel faces were obtained from the Internet (192 novel faces were used for the present experiment from the refresher training to the tests: one per trial, and there were 6 sessions of 32 trials). The faces were all of adult women. All the images were edited using ImageJ software. The images were cropped and the background was white. Brightness and contrast were automatically adjusted to control for differences in lighting conditions. Life-size photographs displayed on the screen were: 25 cm high and 20 ± 2 cm wide.

Procedure

Refresher-Training – *Recurrent Face vs. Novel Portrait Face Presented in Color*

The day before the tests, we checked that all animals reached at least 75% of correct responses (touching one of the four recurrent faces when presented opposite a novel face) over a session of 32 training trials. The procedure was exactly the same as that used in the last step of the training process described above. Horses were rewarded only when they touched the recurrent face.

Tests – *Recurrent Face vs. Novel Face, Presented Under Four Conditions*

Over the 32 trials in one session, 24 were the same as those described for the refresher-training (each recurrent face was presented the same number of times *-i.e., six times-* in a semi randomized order). The other eight (test trials) consisted of presenting the photograph of a novel face opposite one of the recurrent faces, but taken under four different conditions (one condition per session, one session per day): profile, black and white, with large dark sunglasses hiding the eyes and with a wig changing the hairstyle (**Figure 1**). For the wig, if the person had brown hair, we chose a blond wig, and if she had short hair, we chose a long wig (and vice versa). For each test trial, both faces (novel and recurrent) were presented under the same condition (e.g., both wore the same glasses or had the same hairstyle). These test trials were interspersed among the training trials in a semi-random fashion (never more than twice consecutively and balancing presentation of the four recurrent faces between the left and right side of the screen). During the test trial, the four recurrent faces were presented the same number of times (i.e., twice for each condition). Importantly, during the training trials only the recurrent face was rewarded, whereas during the test trials rewards were given for both images (recurrent and novel faces), the aim of the tests being to determine the horse's spontaneous choice without creating a learning bias to touch the recurrent rather than the novel face. This reward system is classically used in the literature (e.g., Pokorny and de Waal, 2009; Lansade et al., 2020), whereas the alternative, that is to say no reward would have led to a rapid extinction of the response.

Control - *Novel Face vs. Novel Face*

A control test in one session was conducted the day after the last test to check that the horses' recognition of the recurrent faces was based on the familiarity of the recurrent face rather than on other clues (for details: Lansade et al., 2020). The procedure was identical to that described above for the tests, but this time, instead of the recurrent face, the face of a novel person was presented opposite another novel face, during the 8 probe trials, intespersed among 24 training trials.

Real Person – *Recurrent Person vs. Novel Person*

Each horse carried out four choice tests (two consecutive tests on two consecutive days). For each test, two experimenters were positioned in two opposite corners of the test area (**Figure 1**). One of them was the recurrent person whose photograph had been used as the recurrent face, the other a person unknown to the horses. The recurrent and the novel person were different for each test, so that eight different people (four recurrent people and four novel people) were mobilized for each horse. For a given horse, choice test 1 involved recurrent person 1 opposite novel person 1; choice test 2, involved recurrent person 2 opposite novel person 2, etc. The position and the order of presentation of the people were counterbalanced between the horses and the tests. An assistant released the horse into the area and waited outside. The experimenters then attracted the horse's attention: they bent the upper part of their body forward while looking at the horse, stretching out their hands and rubbing the thumb and other fingers together every 5 s while making a "kissing" noise with their lips until the horse made a choice or for a maximum of 30 s. They previously practiced to synchronize their movements. Importantly, neither the assistant nor the experimenters were aware of the hypothesis being tested or whether they were a recurrent person or not. At the end of each test, the horse was led out of the test area by the assistant. For each of the tests, three responses were possible: the horse (1) did not touch anyone, (2) touched the recurrent person, or (3) touched the novel person.

Data Analyses

Data were analyzed with XLSTAT software. The data from the refresher-training, the tests and the control were analyzed using Student's *t*-tests to compare the overall performance of the 11

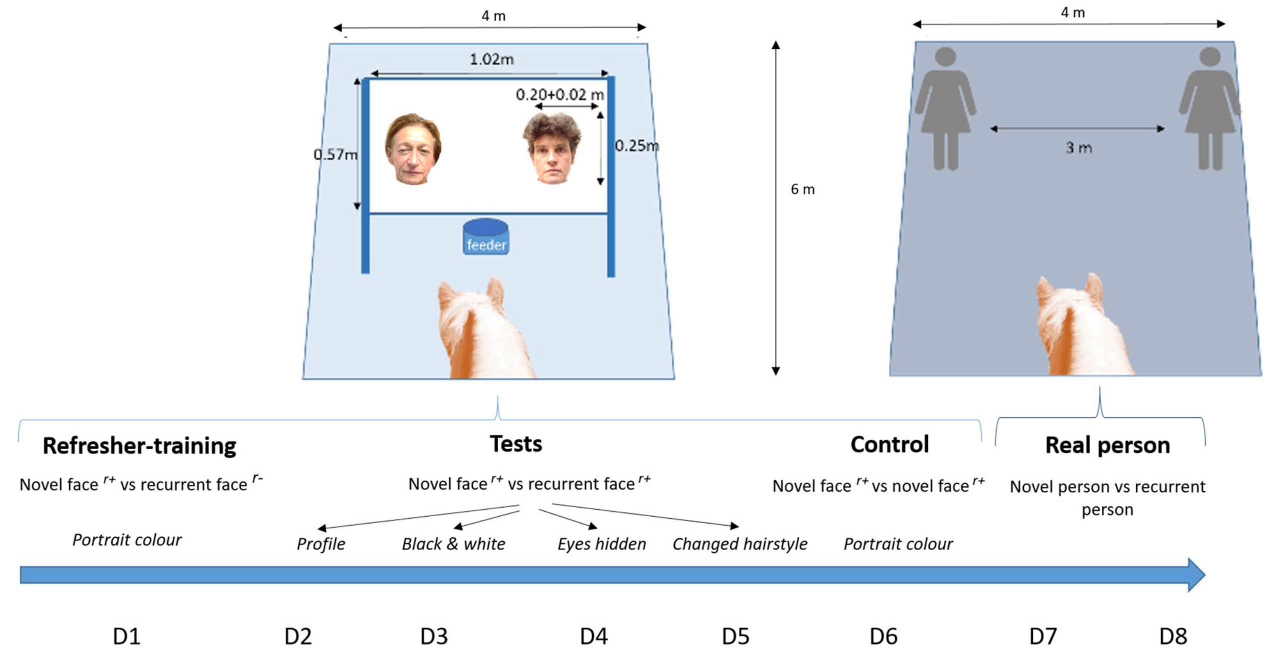

FIGURE 1 | Experimental set up. r^+, reward (pellets); r^-, no reward; D, day.

horses –i.e., the number of correct responses out of 32 trials (refresher-training) or 8 trials (tests and control) – to chance level (50%). A paired *t*-test was used to compare the performance between the four conditions. The data was analyzed only at the overall level and not at the individual level, due to the insufficient number of trials conducted per individual and per condition (only eight trials). Nevertheless, a descriptive analysis of the individual data is presented in the results.

In front of the screen, animals always made a choice. This is not the case for the choice tests with real people. Thus for these we considered only the tests during which the horse made a choice (horses made a choice in median[Q1;Q3]: 3.5[3;4] tests out of the 4 conducted). We then calculated the percentage of tests for which the horse approached the recurrent person out of the number of tests for which the horse made a choice. A Student's *t*-test was used to compare this percentage to the chance level (50%).

A modified Bonferroni correction (Keppel, 1982) was applied to consider the 13 comparisons conducted in the whole study, which were above the significance level from 0.05 to 0.02 ($\alpha_{MB} = df_A\ (\alpha_{PC})/c$ where α_{MB} *is the* Modified Bonferroni, df_A is the degrees of freedom, α_{PC} is the usual alpha level (0.05) and c is the number of comparisons). $N = 11$, except for the "profile" condition during which a horse had to be led back to its stable due to noise outside the test area, and for the test with real people due to a horse requiring veterinary treatment following a minor injury ($N = 10$). The percentage of correct responses per condition and per animal are presented in **Supplementary Table S1**, with the variation coefficient of each variable.

RESULTS

Refresher-Training

Horses' performances were significantly above chance during the refresher-training session ($t = 17.35$, $p < 0.0001$, $n = 11$, **Figure 2**).

Tests

The performances during the tests remained significantly above chance whether the recurrent face was presented in profile ($t = 5.51$, $p < 0.001$, $n = 10$), in black and white ($t = 7.47$, $p < 0.0001$, $n = 11$), with eyes hidden ($t = 4.50$, $p = 0.001$, $n = 11$) or with changed hairstyle ($t = 3.54$; $p = 0.005$, $n = 10$, **Figure 2**). There was no difference in performance between the four conditions (**Table 1**). The descriptive analysis of the individual data in **Supplementary Table S1** indicates that out of the 43 scores (11 animals * 4 conditions, with one piece of data missing), 38 were above and only one below chance level. When focusing on individual by individual, 7/11 animals had scores systematically above chance whatever the condition, whereas only 1/11 had a score below chance, and in one condition only (animal number 5).

Control

As expected, the performances during the control trial were not significantly different from chance level ($t = 0.43$; $p = 0.68$, $n = 11$, **Figure 2**).

Real Person

Horses chose significantly more frequently the recurrent person than at a chance level ($t = 3.18$, $p = 0.011$, $n = 10$, **Figure 2**).

DISCUSSION

This study shows that, when considering all the horses together, face recognition performance remained significantly above chance level whatever the condition tested. The horses were also able to transfer face recognition learned on a screen to a test involving people in real life.

Before discussing the results further we will deal with a certain number of possible biases linked to this type of study. Firstly, as the horses were rewarded for whichever face they touched during the tests trials, we can exclude the effect of rapid learning of the recurrent face during the tests. This bias is discussed in Knolle's study on sheep (Knolle et al., 2017). Another possible bias concerned the fact that we took the images of the recurrent faces while the novel faces came from the internet. Horses could have based their choices on similarities or differences between these two categories, even though all the images had been controlled in terms of contrast and light intensity. In the control test, using a photograph that had been taken with the same camera and under the same light intensity as the recurrent faces, the horses detected it simply as a photograph of an unknown person. This suggests that they did not base their recognition on how the image had been taken and confirms previous findings in another control test (Lansade et al., 2020). The choice with real people also enabled this possibility to be definitively excluded. Finally, the control test also eliminated horse choice relying on the fact that one photograph appeared several times in a row in the same session. Having excluded these biases, we can now discuss the two main findings of this study.

The first notable result is that when considering all the animals together, the horses' performances remained significantly above chance level whatever the condition tested. Under the profile condition, the horses demonstrated a transfer from a front portrait to the same face in profile. Nevertheless, we observed a decrease in performance, similar to that observed in humans (Bruce and Young, 1986) or sheep (Knolle et al., 2017) under the same conditions. Overall performances also remained above chance level for the black and white photographs of the faces, which is also consistent with findings in sheep (Knolle et al., 2017). Horses therefore do not base their recognition solely on an easy clue such as color. Other than color, another plausible hypothesis is that horses simply recognize people from their hairstyle. However, in the condition with the wigs, overall performances were also above chance level, indicating that for most of the horses recognition was not based only on easy external clues such as the hairstyle. Although hair remained an important factor in recognition because it was under this condition that performances were the lowest (although not significantly). It was also under this condition that one individual had the lowest score. This is consistent with the literature on humans: recognition of a novel face is associated with a

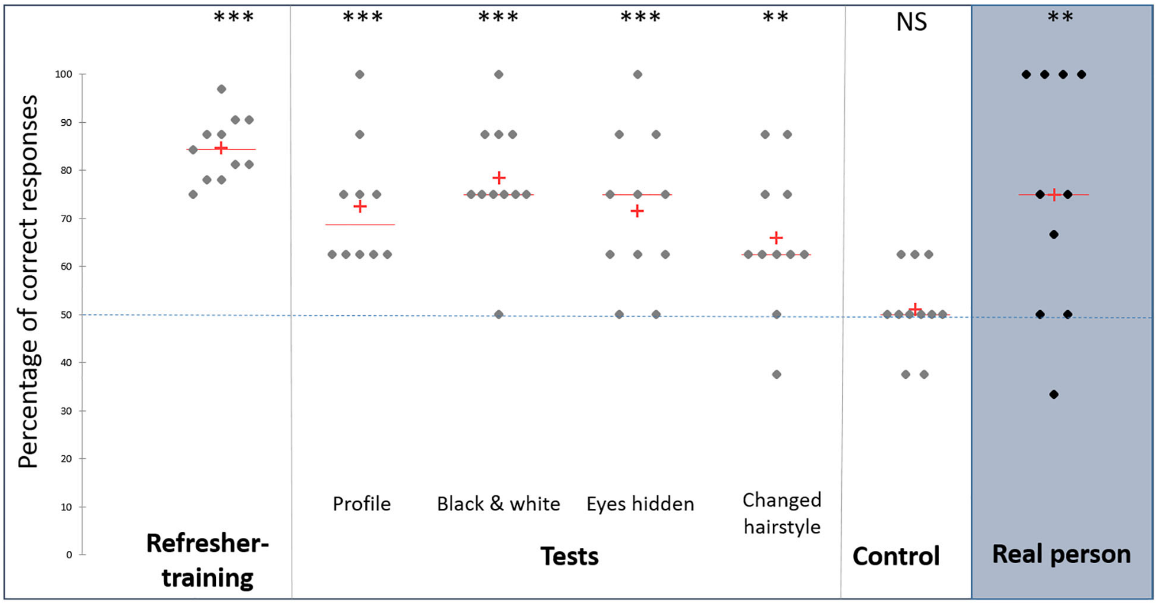

FIGURE 2 | Percentage of correct responses. NS, non-significant; $^{**}p < 0.01$; $^{***}p < 0.001$, Student's *t*-test, calculated according to the level of chance (50%), $n = 11$ except for the profile condition and real person test ($n = 10$). ◆: individual, +: mean, ____: median, — — — —: level of chance.

significant increase in the time spent looking at the external features, such as hair (Logan et al., 2017). Finally, the eyes were not an indispensable element for recognition. Certain studies in humans have suggested that eyes are one of the most important features for facial recognition (Hjelmas and Wroldsen, 1999), while others have shown that they are less relevant, particularly for novel faces, because they are affected to a greater extent by facial dynamics (Logan et al., 2017). This appears to be the case in horses.

The data were not analyzed statistically at the individual level due to the low number of trials carried out per individual and per condition (only eight). This choice of few trials, which is common for this type of study (e.g., Knolle et al., 2017; Lansade et al., 2020) was made to limit any potential learning during the tests. However, a descriptive analysis of the individual data confirms that the animals did not base their choice on one and the same prominent clue to identify the recurrent faces. This analysis also shows that for some of the animals, certain features could be more important than others, but these vary according to the subject. This would suggest that there is a certain inter-individual variability in the way subjects process human faces. This could potentially be linked to differences in personality, which would be an interesting avenue to investigate given the possibilities that exist to test personality in horses (Lansade et al., 2016).

TABLE 1 | Inter-conditions comparison.

	Black and white	Eyes hidden	Changed hairstyle
Profile	$t = -1.24$, $p = 0.24$	$t = 0$, $p = 1$	$t = 1.26$, $p = 0.24$
Black and white		$t = 1.26$, $p = 0.24$	$t = 2.14$, $p = 0.06$
Eyes hidden			$t = 0.70$, $p = 0.50$

t-test for two samples.

Overall, it can therefore be assumed that for the majority of animals facial recognition was holistic in nature rather than being based on one prominent clue, even though certain individuals may privilege a specific feature. Other further studies are required in order to deepen our understanding of holistic face processing in horses. For example, it would be interesting to test a composite or inversion face effect, as already investigated in humans (Nakabayashi and Liu, 2014; Murphy et al., 2017) or other animal species (Burke and Sulikowski, 2013). It would also be interesting to test the horses with the profile of faces with eyes hidden, because horses have laterally positioned eyes and so might pay more attention to a single eye than to two eyes. Finally, further research could investigate the recognition of known individuals in real life, rather than of unknown people as in the present experiment: in humans, external features (e.g., hair) could be the most important factor for facial recognition of strangers (as suggested here), but not for recognizing known faces (Meinhardt-Injac and Persike, 2009; Logan et al., 2017).

The second notable result is that the horses made the connection between the learned photographs and people during the test with a real person. This ability to transfer learning of a face in two dimensions to a test under real conditions (three dimensions) supports Stone's findings in a study using a less complex paradigm, consisting of only two sets of photographs and testing only four horses (Stone, 2010). Through this validation, we demonstrate that the horses in our study did not simply learn to discriminate between two abstract images in two dimensions, but they probably processed the image as a human face. To obtain a greater understanding of how horses process facial images, electroencephalograms could be conducted while testing horses in this type of task, to determine the mechanisms involved and to compare them with those implemented in other common species such as humans, dogs and monkeys (Tsao et al., 2008; Dilks et al., 2015).

CONCLUSION

There would not appear to be one specific element of the face on which all the horses based their facial recognition. Although external features, such as hairstyle, seem to be important in identifying a novel person, horses are capable of using other cues, in particular internal features of the face itself, suggesting holistic recognition of human faces in the majority of individuals. Results also suggests a certain inter-individual variability in how faces are processed which merits further investigation. Finally, horses make a clear link between faces learned on a screen and people in real life, which indicates that they do not process facial images as simple abstract shapes. This knowledge in a non-primate model contributes to improving understanding of phylogenetic evolution of facial recognition processes.

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 Le Comité d'Éthique en Expérimentation Animale Val de Loire (CEEA VdL), France, reference number: 19.

AUTHOR CONTRIBUTIONS

LL devised the study and developed the experimental procedure with VC, CP, and LC. LL, CP, and FR conducted the experiments. LL wrote and revised the manuscript with significant input from VC, AB, and LC. All the authors approved the final version of the manuscript and agreed to be held accountable for the content.

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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.2020.575808/full#supplementary-material

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Horses Solve Visible but Not Invisible Displacement Tasks in an Object Permanence Paradigm

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A key question in the field of animal cognition is how animals comprehend their physical world. Object permanence is one of the fundamental features of physical cognition. It is the ability to reason about hidden objects and to mentally reconstruct their invisible displacements. This cognitive skill has been studied in a wide range of species but never directly in the horse (*Equus caballus*). In this study, we therefore assessed the understanding of visible and invisible displacements in adult Welsh mares in two complementary experiments, using different horses. In experiment 1, visible displacement was investigated using two tasks adapted from the Uzgiris and Hunt scale 1. Invisible displacement was assessed using a transposition task, in which food was first hidden in one of two containers and the location of the containers was then switched. In experiment 2, we further investigated horses' understanding of visible and invisible displacements using an easier procedure designed to avoid potentially confounding factors. In both experiments, horses successfully completed the tasks involving visible displacement with two or three possible hiding places. However, in both experiments, horses failed the transposition tasks, suggesting that they may not be able to track the displacement of an object that is not directly perceived (i.e., invisible displacement). These results bring new insights into object permanence in horses and how they represent their physical world.

Keywords: *Equus caballus*, object permanence, transposition task, secondary representation, invisible displacement, cognition

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INTRODUCTION

A key question in the field of animal cognition is how animals comprehend their physical world. Object permanence is one of the fundamental features of physical cognition. It is the ability to consider objects as independent entities that continue to exist even when they are out of sight (Piaget, 1954). It allows organisms to retrieve hidden objects or to reason about the unseen displacement of objects or conspecifics (Piaget, 1954; Shettleworth, 2009). Hence, object permanence seems important for daily survival of animals, as it may be necessary for key activities such as retrieving food in food-storing species but also hunting prey, avoiding predators, or keeping track of conspecifics in social animals (de Blois et al., 1998; Zucca et al., 2007; Auersperg et al., 2014; Jaakkola, 2014). Better knowledge of these cognitive abilities in domestic animals will help improving their housing and management. Indeed, current husbandry conditions usually involve numerous opaque barriers blocking animals' vision of their surroundings (e.g., walls of stalls or of inside riding areas, transportation vehicles, etc.; Nawroth et al., 2019). A limited understanding of object permanence might thus induce fear reactions, the major cause of horse-related accidents (*Equus caballus*; Keeling et al., 1999), for example, by impacting the predictability of their environment or causing stress due to visual isolation from conspecifics. More generally, a better knowledge of the cognitive abilities of domestic animals could also help change how society perceives them and increase public awareness of welfare issues.

The concept of object permanence was introduced by Piaget (1954), who defined six stages of increasing complexity (**Table 1**). Stage 5 and below characterize the understanding of "visible displacements," i.e., the object is visibly placed in its final location. Stage 6 corresponds to the understanding of "invisible displacement," i.e., the object is first hidden in a displacement device and then invisibly transferred to its final location (typically inside a container or behind a screen). The displacement device is then removed and shown to be empty, enabling the subject to infer that the object has been left in this final location. Solving invisible-displacement tasks is much more demanding, as it requires mentally reconstructing the unseen displacement of the object, thereby involving secondary representations (i.e., the mental representation of an event that was not perceived directly; Suddendorf and Whiten, 2001; Jaakkola, 2014). Recently, an alternative task testing for this understanding of invisible displacement has gained attention in the field of animal cognition (for example, see Doré et al., 1996; Barth and Call, 2006; Hoffmann et al., 2011; Auersperg et al., 2014; Nawroth et al., 2015) called the transposition task. In this task, first introduced by Sophian (1985), the subject can see an object being placed into one of several opaque containers, and the containers themselves are then displaced. The subject has to track the trajectory of the hidden object. This task has the advantage of requiring considerably less memory and attention than the Piagetian task (de Blois et al., 1999; Fiset and Plourde, 2013).

TABLE 1 | Description of the different stages defined by Piaget (1954).

Stage	Description
1	Unable to follow the movement of a visible object
2	Start tracking moving objects
3	Retrieve partially hidden items
4	Retrieve completely hidden items, but commit A-not-B error *A-not-B error*: if an object is repeatedly hidden in a place (A), and is then placed in another location (B), in full view of the subjects, they persevere in choosing the previously reinforced location A
5a	Retrieve an object that is hidden in a different location every time
5b	Retrieve an object that sequentially visits one or several locations before reaching its final hiding location
6a	Retrieve an object that is invisibly transferred directly from a displacement device to the final hiding place (i.e., single invisible displacement)
6b	Retrieve an object that visits one or several other hiding locations in a displacement device before being transferred to the final hiding place (i.e., double or sequential invisible displacement)

Previous results suggest a full understanding of object permanence up to Stage 6 in several non-human species, including primates (e.g., Neiworth et al., 2003; Mendes and Huber, 2004; Barth and Call, 2006), corvids (Corvidae, e.g., Bugnyar et al., 2007; Hoffmann et al., 2011), psittacids (Psittacidae, e.g., Pepperberg et al., 1997; Auersperg et al., 2014; Bastos and Taylor, 2019), pigeons (*Columba livia domestica*, Zentall and Raley, 2019), and goats (*Capra aegagrus hircus*, Nawroth et al., 2015; Vas et al., 2019). Other species succeeded in tasks involving Stage 5, but not 6. These include rhesus monkeys (*Macaca mulatta*, e.g., de Blois and Novak, 1994), prosimians (e.g., Deppe et al., 2009; Mallavarapu et al., 2013), dolphins (*Tursiops truncatus*, Jaakkola et al., 2009; Singer and Henderson, 2015), dogs (*Canis familiaris*, e.g., Collier-Baker et al., 2004; Fiset and LeBlanc, 2007, but see also Gagnon and Doré, 1992, 1993, 1994), macaws (*Ara militaris*, Wrape and Hammonds, 2019), and cats (*Felis catus*, e.g., Doré, 1986; Dumas and Doré, 1989).

The results of several studies suggest that horses (*E. caballus*) can reach Stage 5a of object permanence. For instance, they can remember the location of hidden food (McLean, 2004; Baragli et al., 2011a) and count the number of apples hidden in a bucket (Uller and Lewis, 2009). They also have a precise expectation of the identity of a conspecific once they have seen it disappear to a specific location, suggesting that they still know that individual is there even though they can no longer see it (Proops et al., 2009). However, object permanence has never been directly investigated in horses and, in particular, nothing is known about their understanding of invisible displacements. This is an important gap in our understanding of their physical cognition, especially considering its importance in terms of animal welfare. Hence, in this study, we aimed to investigate further the understanding of object permanence in horses in two experiments. In the first, we used two classical visible-displacement tasks adapted from Uzgiris and Hunt (1975) scale 1 tasks, consisting of hiding an object inside one of two and then one of three opaque containers, and a double-crossed transposition task (Sophian, 1985), testing for the horse's understanding of invisible displacements. The performance of our subjects in this first experiment was poor; we therefore constructed new tasks, which were more straightforward for the horses in a second experiment. (1) We gave them previous experience of containment of an object, by training them to retrieve objects displaced in transparent containers before testing them in visible and invisible displacement tasks. Indeed, this previous visual experience has been suggested to enhance object permanence abilities in adult dolphins (*T. truncatus*; Pérez-Manrique and Gomilla, 2018). (2) During these training sessions, horses were also familiarized with the tasks and their purpose of choosing the baited container in order to receive the food. (3) The experimenter was totally hidden in a hut to make sure the horses focused on the task, rather than trying to use potentially confounding cues from the experimenter's behavior as in the case of Clever Hans study of Pfungst and Rahn (1911). (4) We used a simpler single transposition task, in which only one container was displaced and the initial position of the target was left empty after the transposition.

We hypothesized that the horses would reach Stage 5a of object permanence since previous studies suggest some understanding of visible displacements in horses (e.g., Uller and Lewis, 2009; Hanggi, 2010; Baragli et al., 2011b). Nothing is known about their understanding of invisible displacements.

EXPERIMENT 1

Materials and Methods

Subjects and Husbandry

This study was conducted on 20 female adult Welsh ponies (*E. caballus*, mean age ± SE = 6.60 ± 0.79), bred at the French National Institute for Agricultural Research (INRAE, Nouzilly, France, PAO, doi: 112 10.15454/1.5573896321728955E12), were used for this study. Following a pre-test 16 horses took part in the test, one of which did not take part in the three-bucket task for practical reasons unrelated to this study (cf. 2.1.4).

During the experiment, the horses were housed indoors in groups on straw bedding. They were fed with hay and had access to water ad libitum. None of the horses had previously experienced a procedure similar to the one used in this study.

Ethical Note

This experiment was conducted under the authorization of the French Ministry of Agriculture (File number: 2016110908285740; this study was exempted from research ethics committee approval, as no interventions were applied to the animals). At the end of the experiment, the animals returned to normal breeding at the INRAE experimental unit. No invasive or stressful procedure was performed on them. No obvious injury or sign of pain was observed either. The horses lived in social groups and were taken to an outside paddock daily. During the experimental period, the animals were not subjected to any feed restrictions and were tested in a familiar place.

Procedure

During the different tasks, an assistant held the test horse loosely on a leading rein with their back toward the horse, while an experimenter handled the bucket(s) (**Figure 1**). The horse stood with its head passed between the vertical bars of a fencing panel (spacing = 0.50 m) of a 12 × 12 m stall, so that it could move its head freely but could not move forward. In all tasks, food pellets were hidden alternately in one of two or three buckets in an order randomized between the horses for six trials. During the baiting, the buckets were out of the horse's reach, approximately 1 m away; they were then closed with a lid and pushed toward the horse simultaneously. The first bucket the horse touched was defined as the chosen bucket. We considered that the horse made a choice if it touched a bucket with its nose in less than 30 s; otherwise, the trial was marked as uncompleted and a new trial started (no trial had to be restarted more than twice).

The buckets used were green plastic buckets (0.20 m in diameter and 0.10 m deep), closed by a green plastic lid. This type of bucket was unfamiliar to the horses before the beginning of this experiment. Each bucket was composed of two recipients, stacked together with food in between to create a false bottom. Horses could thus not find the target bucket by using their sense of smell, as all buckets actually contained food.

Tests

Before the actual test phase, we started with six pre-test trials to ensure that the horses were motivated and to familiarize them with the buckets. In the first three trials, the experimenter put food pellets in a bucket, half-closed it with a lid, and then placed the bucket on the ground approximately 0.65 m from the horse. The procedure of the three last trials was identical except that the bucket was completely closed with the lid. The horses passed a trial by directly touching the lid of the bucket within 30 s in an attempt to reach the food. The experimenter then opened the lid and let the horse eat. Only the horses that succeeded in all of the pre-test trials took part in the tests (i.e., 16 out of 20 horses).

The different tasks are summarized in **Figure 2**. All tasks were videotaped using a Sony DCR-SR21E camera. The pre-tests were performed in one session, whereas the three test tasks were performed on 3 separate days to reduce the duration of the sessions so that the horses did not lose concentration or motivation for food. The two-bucket task was carried out first,

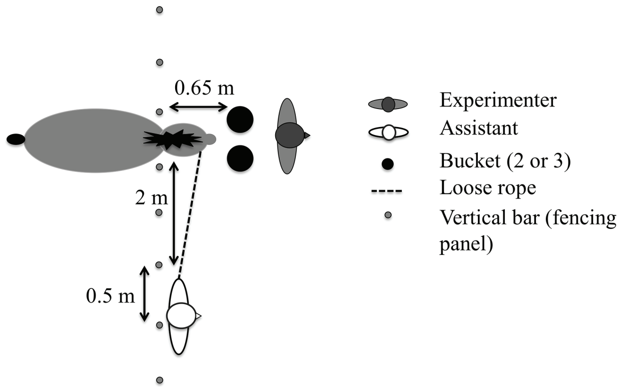

FIGURE 1 | Experimental set-up. The small triangles represent the experimenter's and the assistant's noses: both of had their backs to the horse. All distances are approximate.

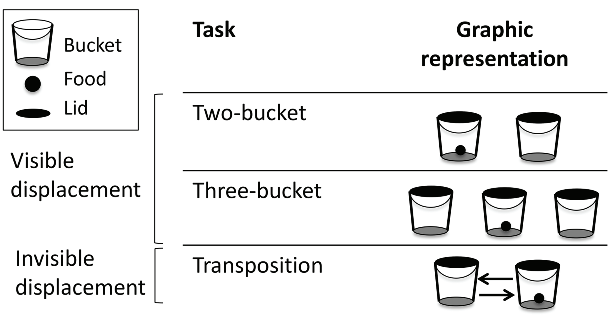

FIGURE 2 | Graphic representations of the different tasks.

then the transposition task and finally the three-bucket task. The risk of associative learning, through which the horse could learn how to solve the task by using a simple associative rule rather than object permanence (Jaakkola, 2014) was prevented by reducing the total number of trials performed and conducting each task in only one session.

1. The two-bucket task. The experimenter put the food in one of the two buckets, placed approximately 0.50 m apart at equal distance from the horse. The assistant and experimenter had their backs to the horse to prevent accidental social cueing. The experimenter interacted similarly with both buckets avoiding any attention bias of the horse toward the baited bucket by putting one hand above each bucket and then opening her hands, to drop the food pellets into one of the buckets. In addition, the two lids were closed at the same time.
2. The three-bucket task. This task was similar to the two-bucket task, except that it involved three buckets placed next to each other approximately 0.30 m apart. In this task, the experimenter had to face the horse for practical reasons, but wore a scarf on her face to hide her eyes and facial expression. Again, while placing the food pellets inside a bucket, the experimenter put her second hand above another bucket at the same time so as not to point toward one bucket in particular during the baiting. The experimenter first closed two lids and then the third one; the order in which the lids were closed was randomized. To allow the three buckets to be pushed toward the horse at the same time, they were placed on a large piece of cardboard, and the cardboard was moved.
3. The transposition task. The food pellets were again hidden in one of the two buckets (cf. two-bucket task), but then the position of the two buckets was swapped so that the left bucket was now located on the right-hand side and the right bucket on the left-hand side. Again, the experimenter had to face the horse during this task, but wore a scarf over her face. During the swapping, the right bucket always passed in front of the left bucket, independently of where the food was.

Statistical Analyses

The horse successfully completed a trial by touching the baited bucket first. For each horse, the number of successful trials over the six trials was calculated from the video recordings.

All statistics were performed with R 3.0.2 (R Core Team, 2013). Due to our limited sample size, we used nonparametric statistical tests. All of the tests used were two-tailed.

For each of the three tasks, we used a one-sample Wilcoxon signed-rank test to determine whether, at the group level, the proportion of successful trials obtained by each individual over the six trials differed from chance level (fixed at 0.50 for the two-bucket and the transposition tasks and at 0.33 for the three-bucket task).

Results

All the results from the different tasks are summarized in **Table 2**.

Two-Bucket and Three-Bucket Tasks

Horses chose the correct bucket more often than expected by chance when tested with two buckets [$N = 16$, $M = 0.62$, 95% CI (0.50, 0.83), $V = 52$, $p = 0.013$] and with three buckets [$N = 15$, $M = 0.49$, 95% CI (0.33, 0.67), $V = 54$, $p = 0.006$].

Transposition Task

Horses did not choose the baited bucket significantly more often than expected by chance [$N = 16$, $M = 0.56$, 95% CI (0.50, 0.67), $V = 28.5$, $p = 0.156$)]

Summary

In the two-bucket and the three-bucket tasks, horses were able to retrieve an object (here, food) that had been hidden in two or three different locations in several successive trials, reaching Stage 5a of object permanence. However, even though they chose the baited bucket significantly more often than expected by chance as a group, the mean proportions of success of the horses were not very high. Moreover, horses failed to choose the baited bucket more often than expected by chance in the transposition task. Hence, our results do not support that horses can reach Stage 6a.

Their poor performances in these tasks could be explained by different factors. (1) Our subjects could lack experience with hidden objects, as they might not have had a lot of opportunities to interact with hidden objects in their life. Indeed, in infants and chicks it has been suggested that such interactions can be important for the development of object permanence (Bremner et al., 2015; Prasad et al., 2019).

TABLE 2 | Performance of each horse in the different tasks. Results are given as the number of successful trials over the total number of trials.

Individuals	Number of successful trials/total number of trials		
	Two-bucket	Three-bucket	Transposition
Flavie	4/6	2/6	4/6
Fantasy	4/6	3/6	3/6
Filharmonie	3/6	2/6	3/6
Furibonde	3/6	4/6	3/6
Forever	5/6	2/6	4/6
Elegante	5/6	4/6	3/6
Estampe	5/6	4/6	3/6
Eloge	3/6	2/6	4/6
Eclipse	4/6	2/6	3/6
Dolly	2/6	4/6	1/6
Diva	2/6	1/6	4/6
Danseuse	3/6	X	2/6
Cybele	3/6	3/6	3/6
Berenice	6/6	4/6	5/6
Valentine	3/6	3/6	3/6
Victoria	5/6	4/6	6/6
N	16	15	16
Mean proportion of success	0.62*	0.49*	0.56^{NS}
Chance-level	0.50	0.33	0.33

"X" indicates that the horse could not be tested for practical reasons.
Significance was assessed by a Wilcoxon signed-rank: $^{NS}p > 0.05$; $^{*}p \le 0.05$.

Giving the horses opportunities to interact with hidden objects prior to testing them in the different tasks might increase their performances, as has been shown in adult dolphins for instance (*T. truncatus*; Pérez-Manrique and Gomilla, 2018). (2) Horses might have not been familiar with the purpose of the task, namely that they had to choose only one bucket and that if they chose the baited bucket they could eat the food inside. (3) Instead, horses might have sought to use a rule based on the experimenter's behavior, as in the case of Clever Hans (Pfungst and Rahn, 1911). As the experimenter took the utmost care not to indicate the baited bucket, the arbitrary social cues horses could use might have been confounding and could have hinder their performance in the task. (4) The crossed-transposition task can be confounding for some species (e.g., in dogs, *C. familiaris*; Miller et al., 2009) because the two containers are displaced at the same time, which can be distracting for the subject, and because there is a lack of visual change between the final situation after transposition and the initial situation prior to transposition.

Hence, we carried out a second experiment with different horses and a different protocol in an attempt to address these potential issues. (1–2) Horses were first trained to retrieve a food reward hidden in a transparent container, before testing them in visible and invisible displacement tasks. (3) The experimenter was completely hidden from the horse in a hut. (4) We used a single transposition task: only one cup was displaced at a time and the initial position of the target was left empty after the transposition.

EXPERIMENT 2

Materials and Methods

Subjects and Husbandry

This experiment was conducted on 14 other female Welsh ponies from 6 to 9 years old (mean age ± SE = 7.90 ± 0.31). From these 14 horses, 10 were used in the two-cup test and six in the three-cup test because the other horses did not reach the success criterion during the training sessions. For practical reasons, the experiment had a limited time period in which to conduct the test, and therefore only three horses (Ukraine, Uppsala, and Ballerine) finished the three-cup test quickly enough to be trained and tested in the single-transposition (ST) test.

Apparatus and General Procedure

The apparatus consisted of a sliding wooden tray (1.40 × 0.60 m), placed on a table (1.80 ml × 1.20 mw × 0.57 mh; cf. **Figure 3**). The tray could be slid by the experimenter from an adjacent hut, using a handle (0.84 m long). The experimenter and the assistant were hidden in this hut (2.30 × 1.07 × 1.86 m) during the entire duration of the test session in order to avoid social cueing. Both could see the horse through two tinted-glass windows and the experimenter could pass her hands through two small holes (0.27 × 0.15 m, hidden by black fabric) to place and manipulate the experimental material on the tray. The tray was divided into three compartments (each 0.28 m wide) by four pairs of wooden bars: one on the left (compartment L), one in the middle (compartment M), and one on the right (compartment R).

During the experiment, the horse was loosely attached with a leading rein in front of the apparatus. The experimenter first attracted the horse's attention by knocking on the window of the hut. In full view of the horse, a food reward was placed by the experimenter into one of the three compartments (approximately 1.00 m away from the horse) and two or three green, opaque, plastic cups (0.06 m in diameter and 0.09 m high) were placed on the tray, one per compartment and with one of them hiding the reward. Prior to this experiment, the horses were unfamiliar with these cups. We chose to use cups instead of buckets, as cups were easier for the experimenter to handle from inside the hut. A food reward was stuck at the bottom of each cup, to control for sensory cues. The experimenter then pushed the sliding tray toward the horse, so that the horse could pass its head between the wooden bars, into the appropriate compartment, knock over the plastic cup and eat the reward. The test and training sessions consisted of several of these trials in a row: the location of the reward during each trial was semi-randomized, so that it was never hidden in the same compartment more than twice in a row. The risk of associative learning was reduced by interacting similarly with the different cups.

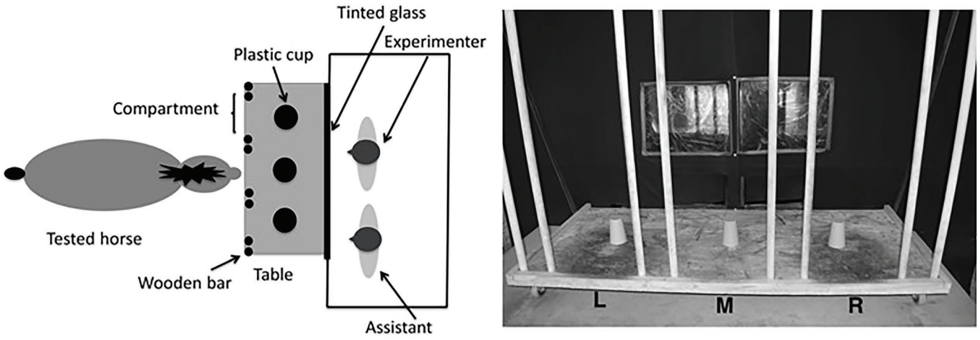

FIGURE 3 | Arrangement of the experimental apparatus. On the left, a schematic representation shows how the horse and the experimenters were located around the apparatus. The small triangles represent the experimenter's and the assistant's noses: both of them faced the horse. On the right, a picture shows the sliding tray, divided into three compartments by wooden bars (L, M, and R). The three plastic cups are arranged as they were for the three-cup test.

The horses were tested individually, 5 days a week, typically twice a day during 8–10-min sessions (either test sessions or training sessions). Four different test types were carried out as described below.

Training

Each test was preceded by a training period, including specific training for this test type and basic training. This training aimed at providing horses with visual experience of hidden objects. Moreover, during the specific training, horses learned to choose one and only one cup to that they had to find the food reward in order to be allowed to eat it. Basic training served to familiarize the horses with the apparatus (the sliding tray and the plastic cups) and then as a means to ensure motivation. The sessions were started with the simple basic training task followed by the more complex specific training task.

Our success criterion to enable a horse to start taking a test was to succeed in the corresponding specific training task for four consecutive sessions over 2 days or for at least five sessions over 3 days.

1. Basic training: find-the-reward training (FR). The reward was placed in one of the compartments and stayed in full view of the horse. The horses received either three trials – if they succeeded in all three – or six trials. They were considered to have succeeded in this task if they passed their head into the baited compartment at the first attempt, either for the first three or for five out of six trials.
2. Basic training: one-cup training (1C). In full view of the horse, the reward was placed into one of the compartments and was then hidden under a single green plastic cup. The number of trials and the success criterion were the same as in the FR training.
3. Specific training: two-transparent-cup (2TC), three-transparent-cup (3TC), and single-transposition training. The general procedure used during these training sessions was exactly the same as the one used during the corresponding tests except that the cups used were transparent. Horses succeeded in this task if they chose the baited cup for five out of six trials.

Horses reached success criterion after 71.1 ± 7.5 (Mean ± SEM) training sessions (corresponding to 35.5 ± 3.7 days) for the two-cup test; after 21.7 ± 9.1 sessions (or 10.8 ± 4.5 days), for the three-cup test; after 28.7 ± 9.7 sessions (or 14.3 ± 4.8 days) for the single-transposition test.

Tests

Three different types of test were performed (**Figures 4–6**).

1. The two-cup test: a food reward was hidden under one of two opaque plastic cups (one in compartment L and the other in compartment R).
2. The three-cup-test: a food reward was hidden under one of three opaque plastic cups (one cup in each compartment).
3. The single-transposition test: a food reward was hidden under one of two opaque plastic cups (placed in two of the three compartments) and one of the cups was then moved to an adjacent compartment.

All the tests were performed over six consecutive sessions, consisting of six trials each, over 3 days. At the beginning of each test session, pre-test training trials were performed in order to ensure horses were attentive and motivated. These pre-test training trials consisted of three or six trials of the 1C and three to six trials of the specific training corresponding to the test (2TC, 3TC, or ST). If the horse failed the pre-test training three times during a session, the session was interrupted and a supplementary test session was added at the end of the 3 days. If more than one test session had to be interrupted in that way, it was considered that the horse did not sufficiently master the training tasks and additional training sessions were added until the horse met the success criterion again.

During the test (and training) trials, the way the food reward and the plastic cups were positioned on the sliding tray was

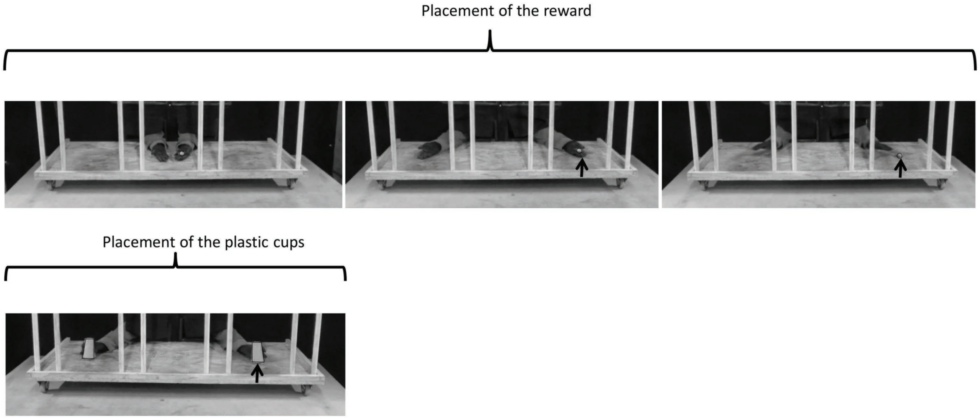

FIGURE 4 | Detailed procedure used for placing the reward and plastic cups during the two-cup test. The outlines of the reward and of the cups have been highlighted to improve their visibility in the pictures. The arrow indicates the location of the reward.

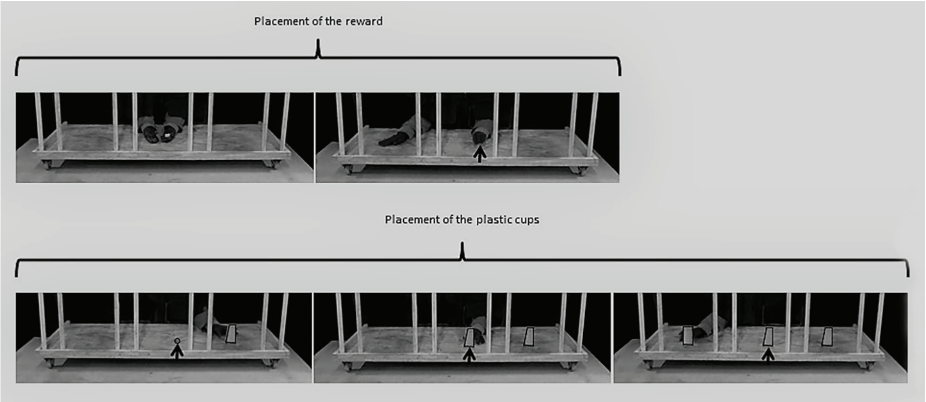

FIGURE 5 | Detailed procedure used for the placing the reward and plastic cups during the three-cup test. The outlines of the reward and the cups have been highlighted to improve their visibility in the pictures. The arrow indicates the location of the reward.

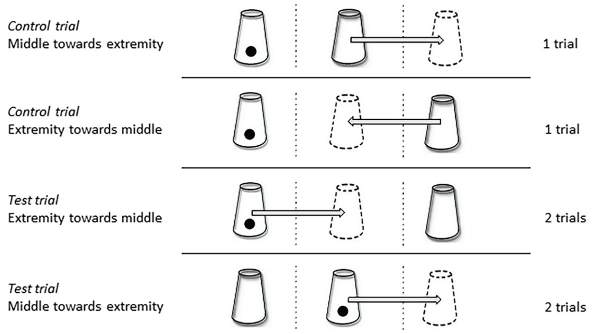

FIGURE 6 | Schematic representation of the four types of trials. The cups drawn in dotted lines represent the final positions of the cup, after transposition; the arrows represent the movement of the cups during the transposition. In "Extremity towards middle" trials, the cups were shifted from the middle to an extremity, while for the "Middle towards extremity" trials the cups were shifted from an extremity to the middle. These four types of trials were randomized during each test session (the number of trials conducted for each type is indicated on the right).

highly standardized and was designed to be symmetrical in order to prevent associative learning.

1. Two-cup test (**Figure 4**):
   - Placing the reward: the experimenter extended her two hands out through the holes in the hut, one of them holding the reward, and showed their content to the horse by opening her hands palm upward, in the middle compartment of the tray. The two open hands (with the reward visible) were then moved simultaneously and symmetrically: the left hand to compartment R and the right hand to compartment L. The experimenter put the reward into the target compartment, and took her hands back inside the hut.
   - Placing the plastic cups: the experimenter took two opaque plastic cups out, one in each hand, and placed them simultaneously and symmetrically in the two compartments, one of them covering the reward. The experimenter then took her hands back inside the hut.
2. Three-cup-test sessions (**Figure 5**):
   - Placing the reward: the reward was placed in exactly the same way as in the two-cup test except that, after extending her two hands palm upward in the middle compartment of the tray, the experimenter moved her hands simultaneously toward two of the three compartments used (the baited compartment and one of the other two which was assigned randomly). The hand holding the reward placed it into the baited compartment, while the empty hand performed exactly the same gesture in another compartment. The purpose of this procedure was to avoid interacting with the baited compartment only, to prevent the horses forming associative rules.
   - Placing the plastic cups: the three cups were placed successively from the right to the left of the horse. The experimenter took the cups out one at a time: she placed the first one into compartment R with her left hand and the two others into compartments M and L with her right hand. She then took her hands back inside the hut.
3. Single-transposition test (**Figure 6**):
   - Placing the reward: the reward was placed in one of the three compartments, using the same procedure as described previously for the three-cup test.
   - Placing the plastic cups: the experimenter took two plastic cups out, one in each hand, and placed them simultaneously in two out of the three compartments (randomly assigned), one of them covering the reward.
   - Displacing the plastic cups: the experimenter shifted one of the plastic cups to an adjacent compartment (so either from the middle – compartment M – toward an extremity - compartment L/R, or from an extremity toward the middle). During this procedure, the experimenter kept the other hand on the motionless cup in order to act in a similar way with the two cups.Two types of trials were carried out. (1) In the

control trials, the displaced cup was empty, while (2) in the test trials, it was the baited cup. Each test session consisted of two control trials (one in which the cup was shifted from the middle to an extremity and the other from an extremity toward the middle) and four test trials (two of each type), carried out in a random order.

Statistical Analyses

Horses were considered to have chosen a specific compartment if they moved their head into this compartment first and fully extended their head between the wooden bars of this compartment.

Horse performances at group and individual levels were assessed through the following procedures:

1. Two-cup and three-cup tests: the number of successfully completed trials for the entire test (i.e., combining all the sessions, over the 36 trials) was used as a dependent measure for each test.
2. Single-transposition test: the number of successfully completed trials for the test trials of the entire test (i.e., over 24 trials) and the number of successfully completed trials for the control trials of the entire test (i.e., over 12 trials) were used as a dependent measures. Due to the limited sample size ($N = 3$), we could not perform a Wilcoxon signed-rank test at the group level. Therefore, we only tested significance at the individual level. Moreover, for the horses that significantly succeeded in both test and control trials, binomial tests were also carried out to investigate whether they succeeded at an above chance level when considering the extremity-toward-middle trials only or the middle-toward-extremity trials only.

Exact binomial tests were run to compare the individual performance of each horse with chance level (fixed at 0.50 for the two-cup and single-transposition tests and 0.33 for the three-cup test). We used a Wilcoxon signed-rank test to compare the proportion of success of the whole group with chance level.

Results

Two-Cup and Three-Cup Tests

When considered at group level, horses performed significantly above the chance level for the two-cup test [$N = 10$, $M = 0.87$, 95% CI (0.84, 0.91), $V = 55$, $p = 0.006$] and the three-cup test [$N = 6$, $M = 0.70$, 95% CI (0.67, 0.71), $V = 21$, $p = 0.035$; **Figure 7**]. Moreover, all of the horses individually scored significantly higher than expected by chance both in the two- and the three-cup tests (**Table 3**).

Single-Transposition Test

The three horses reached the success criterion during training sessions and thus took the single-transposition test. Two of them (Ukraine and Uppsala) performed significantly better than expected by chance in the single-transposition test trials. Only Uppsala succeeded significantly better than expected by chance in the single-transposition control trials (**Table 3**).

Further binomial tests showed that Uppsala succeeded significantly more often than expected by chance in the extremity-toward-middle trials [success rate = 0.92, 95% CI (0.61, 1.00), $p = 0.006$] but not in the middle-toward-extremity trials [success rate = 0.58, 95% CI (0.28, 0.85), $p = 0.774$].

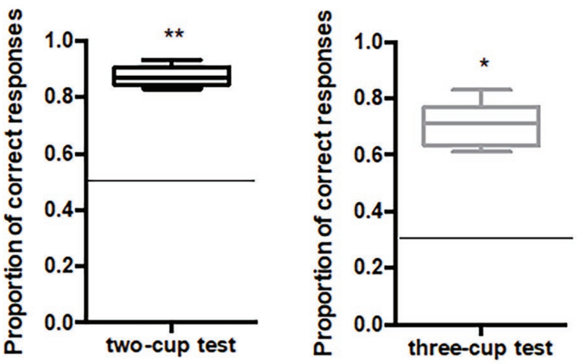

FIGURE 7 | Median proportion of correct responses for the two-cup and the three-cup test. Horizontal lines indicate chance levels (fixed at 0.5 for the two-cup test and at 0.33 for the three-cup test). Deviation from chance was assessed by a Wilcoxon signed-rank test. $^{*}p \leq 0.05$, $^{**}p < 0.01$.

TABLE 3 | Proportion of correct responses for each test, for each individual. Deviation from chance at the individual level was tested by an exact binomial test.

Individuals	Number of successful trials over the total number of trials			
	2-cup test	**3-cup test**	**S.t. test trials**	**S.t. control trials**
Ukraine	$33/36^{***}$	$25/36^{***}$	$23/24^{***}$	$9/12^{NS}$
Uppsala	$32/36^{***}$	$32/36^{***}$	$18/24^{*}$	$12/12^{***}$
Ballerine	$35/36^{***}$	$26/36^{***}$	$16/24^{NS}$	$9/12^{NS}$
Valda	$31/36^{***}$	$25/36^{***}$		
Volga	$30/36^{***}$	$21/36^{**}$		
Aventure	$30/36^{***}$	$24/36^{***}$		
Urielle	$34/36^{***}$	$25/36^{***}$		
Vanille	$31/36^{***}$			
Vaillante	$28/36^{**}$			
Altesse	$31/36^{***}$			
Mean proportion of success	0.87^{**}	0.70^{*}	0.79	0.83
Total number of trials	36	36	24	12
Chance level	0.50	0.33	0.50	0.50

Deviation from chance at the group level was tested by a Wilcoxon signed rank test. S.t stands for "single-transposition (ST)."
$^{NS}p > 0.05$; $^{*}p \leq 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Summary

All of the tested subjects succeeded in visible-displacement tasks (Stage 5a), whether they were tested with two or three possible hiding places.

In the invisible-displacement task (Stage 6a), two out of three horses succeeded in the test, but one of them failed in the control trials, which suggests that it relied on an associative rule (i.e., always choosing the cup that was displaced), rather than understanding visible displacement. The horse (Uppsala) that succeeded in both the test and the control trials did not exceed chance level when the baited cup was moved from the middle compartment toward an extremity. This result suggests that this horse might have used an associative rule as well. Fiset and Plourde (2013), who performed a similar experiment in dogs (*C. familiaris*) and wolves (*Canis lupus*), suggested that they might have succeeded in this task by selecting the container closest to the newly empty baited position instead of solving invisible displacements. This hypothesis could explain the results of Uppsala as well: the middle-toward-extremity trials might have been more difficult for it since both cups were equidistant to the newly empty previously baited compartment. Hence, although the results from this transposition test should be considered with caution because of the low sample size, they do not support the hypothesis that horses comprehend invisible displacement. Nevertheless, most of the horses tested could still use alternative strategies (probably learned by associative learning) to solve the task, which demonstrates their flexibility.

Interestingly, the horses obtained higher proportions of success in the Stage 5a tasks of experiment 2 (two-cup test = 87%; three-cup test = 70%) than in experiment 1 (two-bucket task = 62%; three-bucket task = 49%). Since a previous study shows that horses perform better in visual discrimination tasks when the stimuli were on the ground than at nose level (Hall et al., 2003), we could have expected that horses would have performed better in experiment 1 (when the buckets were on the ground) than in experiment 2 (when the cups were on a table), but this was not the case.

The better results in experiment 2 could be explained by the adjustments made in this experiment compared to experiment 1, and in particular due to the additional training phase, during which horses were trained to retrieve objects placed in transparent containers. This training could have helped the horses to gain more experience with hidden objects. The importance of such previous experience has been shown in dolphins (*T. truncatus*) for instance (Pérez-Manrique and Gomilla, 2018). Moreover, in these training sessions, horses could learn to understand the purpose of the tasks, namely that they had to choose only one cup and to find the food reward in order to be allowed to eat it. The training could also have improved their working memory and attention span. Furthermore, it could be related to the fact that the experimenter was totally hidden in a hut during the experiment 2. This prevented the horses from seeking to use potentially confounding cues from the experimenter's behavior (as in the case of Clever Hans, Pfungst and Rahn, 1911). Alternatively, the large number of training sessions in experiment 2 might have resulted in associative learning: horses could have learned associative rules during the training to find the reward more accurately than in experiment 1, in which they could only rely on their object permanence abilities. We used transparent cups during the training to reduce this possibility: horses could see the content of the cups at all times and thus did not need to develop associative rules to find the food reward. Nevertheless, this cannot be excluded, particularly since the results of the transposition test suggest that they used associative rules.

GENERAL DISCUSSION

We carried out two experiments with different horses. In the first experiment, we used two classic paradigms to test for Stages 5a and 6a of object permanence. In the second experiment, we tested these two same stages with a different protocol designed to make the tasks easier for the horses by avoiding potentially confounding factors. In both experiments, horses were successful in the visible-displacement tasks, whether they were tested with two or three possible hiding places. These results suggest that adult horses can comprehend visible displacement and hence reach Stage 5a of object permanence following the Piagetian framework. However, our horses did not succeed in the transposition tasks, either in experiment 1, or in the simpler version used in experiment 2. Hence, our results do not support that horses understand invisible displacements (Stage 6a of object permanence).

Special care was taken in both experiments to avoid bias due to sensory or social cueing and to limit the risk of associative learning, although the latter cannot be totally excluded in experiment 2, as it involved a large number of training sessions.

Horses Solved All Visible-Displacements Tasks (Stage 5a)

In both experiments, horses succeeded in the tasks involving visible displacement. They were able to retrieve an object that was hidden in two or three different locations in several successive trials (Stage 5a). Our study is thus the first to show directly that horses can understand visible displacement, suggested in several previous studies. For instance, horses were found to be able to remember the location of hidden food (McLean, 2004; Baragli et al., 2011a); to count the number of apples hidden in a bucket (Uller and Lewis, 2009); to ask their caretaker for help to reach a hidden food source (Ringhofer and Yamamoto, 2016; Trösch et al., 2019); and to form a precise expectation of the identity of a conspecific once they saw it disappear to a specific location (Proops et al., 2009). Further studies, testing whether horses can successfully complete a sequential visible-displacement task (Stage 5b) would be interesting to complement our results.

Horses Failed to Solve the Invisible-Displacement Tasks (Stage 6a)

In experiment 1, horses failed to choose the baited container more often than expected by chance in the transposition test. In the single-transposition test of experiment 2 (Stage 6a), some horses succeeded, but seem to have relied on associative rules rather than on an understanding of invisible displacements. As the Piagetian framework and the different tasks used in this study were originally established for humans, we could consider whether horses failed these tasks because of limited object permanence ability or because these tasks are not adapted to horses (Pepperberg, 2002). For instance, we could wonder if horses failed because of an insufficient short-term memory, as transposition tasks require higher short-term memory capacities than visible-displacement tasks since the time between the moment the food item is hidden and the moment the horse can start searching for it is longer due to the time taken for the containers to be displaced (Jaakkola et al., 2009). However, this time period was only approximately 5 s in our study, which is greatly inferior to the working memory duration of 20s reported for horses by Valenchon et al. (2013), who used a similar protocol. Furthermore, as our horses were successful in all of the visible-displacement tasks, the ecological relevance of our experimental set-up or the motivation to find food is unlikely to have been a source of failure. It would nevertheless be interesting to study further how horses understand invisible displacement using a more naturalistic set-up (for instance in the context of the disappearance of a human or a conspecific rather than food). In view of our current results, we thus cannot conclude that horses comprehend invisible displacements. Similar results of failing to comprehend invisible displacements have been found in other species, including dolphins (*T. truncatus*; Jaakkola et al., 2009), dogs (*C. familiaris*; Collier-Baker et al., 2004; Fiset and LeBlanc, 2007), rhesus monkeys (*M. mulatta*; de Blois and Novak, 1994), prosimians (Deppe et al., 2009; Mallavarapu et al., 2013), and cats (*F. catus*; Doré, 1986; Dumas and Doré, 1989). It has been argued that most invisible displacements in natural conditions could actually be partly solved by a reliance on external cues; for example, moving objects or subjects – food items, predators, or conspecifics – can also be detected through the use of other sensory cues, and usually reappear near to where they were last seen by the individual (Jaakkola, 2014). Nevertheless, horses in our study showed that they could flexibly use associative rules to deal with this type of displacements. It is possible that horses are able to comprehend invisible displacements but only rely on this more complex strategy as "a last resort," when there is no easier alternative strategy available. In our experiment, they still received rewards regularly by using simpler associative rules, which might explain why they did not use their ability to understand invisible displacement.

In both experiments, the containers were placed 1 m from the subject during the transposition trial, as horses have been shown to have low visual acuity at distances under 1 m. Nevertheless, in both experiments, there were bars forming a barrier between the subject and the containers, which has been shown to reduce dogs' performances in an object choice task. This phenomenon might also be true for horses and could have decreased their performances. Hence, it might be interesting for further studies to design a different protocol that does not involve a barrier.

Conclusion and Implications for Animal Welfare

To conclude, the results from our two experiments, using different horses and protocols show that horses seem to understand visible displacements. Horses thus reach Stage 5a of object permanence following the Piagetian framework. However, horses failed the transposition tasks, suggesting potential lack of understanding of invisible displacements (Stage 6a).

When considered in a more applied context, our results highlight that horses' perception of the external world, and in particular their reasoning about invisible displacements, differs considerably from our own. Horses seemed to fail in a transposition task that is easily solved by human adults. It is particularly important to take this new information into account as current husbandry methods usually involve walls and opaque barriers that limit the field of view of horses (Nawroth et al., 2019). This incomplete understanding of object permanence might thus increase the unpredictability of their world. For instance, horses might have difficulties in anticipating the re-appearance of objects or individuals that were out-of-sight (Désiré et al., 2002), potentially inducing stress (example in lambs: Désiré et al., 2004). Moreover, being visually isolated from conspecifics could also result in a stressful situation since horses are gregarious animals (Waring, 2003). Addressing these potential stressors in horse husbandry and equestrian practices, could contribute to improving their well-being and reducing the occurrence of horse-related accidents, whose major cause is fear reactions (Keeling et al., 1999).

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 no interventions were applied to the animals (Val de Loire Ethical Committee, CEEA, VDL, France; file number: 2016110908285740).

AUTHOR CONTRIBUTIONS

MT and LL: conceptualization. MT and LL: methodology. LL: validation. MT, AF, and LL: formal analysis. MT, AF, and MC: investigation. LL: resources. MT and AF: data curation. MT: writing – original draft preparation. MT, LL, RN, and LC: writing – review and editing. MT, LL, RN, and LC: visualization. LL: supervision, project administration and funding acquisition. All authors contributed to the article and approved the submitted version.

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Would the Dog Be a Person's Child or Best Friend? Revisiting the Dog-Tutor Attachment

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Among all relationships that a human life comprises, there is often the development of interspecific relationships, especially with dogs (Julius et al., 2013). Dogs can cooperate in various scenarios, as they can guide blind people, herd sheep, rescue people, work in animal-assisted therapy, among other activities (Serpell, 2017); and beyond all operational interactions, most tutors and dogs become attached to each other (we are using the term tutor as a synonym of guardian, the one who takes care of the dog). What do people search for in an affectionate relationship with dogs? Are people searching for a new experience of caring for someone who depends on them for basic needs? For an emotional support in difficult times? For a long-term and consistent relationship, a strong connection, a mutually enjoyable contact? In other words, are people searching for a child, for a best friend or both? And how does it work from the dog's perspective? The Bowlby's theory (Bowlby, 1969) focused on child-caregiver attachment is being used to explain dog-tutor attachment. However, we argue that this approach should be integrated with the human friendship attachment theory and the intraspecific dog attachment. Therefore, it is important to revisit the approach to the dog-tutor attachment.

CHILD-CAREGIVER ATTACHMENT

The attachment bond encompasses behavioral strategies used by individuals to maximize their survival, by balancing two motivational processes: the need for protection from threats and the drive to explore the environment. A dynamic equilibrium of these two motivational processes is important for the child development (Cassidy, 2016). The attachment figure is the individual who offers comfort in stressful situations (*safe haven effect*) and the security to explore the surroundings (*secure base effect*) (Bowlby, 1969; Ainsworth et al., 1978).

In the child-caregiver attachment, two behavioral systems, namely the attachment system and the caregiving system (Julius et al., 2013), are combined to increase the chances of survival of the offspring. The attachment system is activated in children by emotional stress, triggered by internal or external stimuli, and it includes a set of behaviors used to reestablish the proximity with the caregiver such as calling, crying, etc. The caregiving system is activated in the caregiver by the perception of danger or by the child showing attachment behaviors. Julius et al. (2013) emphasizes that, when child and caregiver interact in synchrony and work together to maintain proximity, both systems are successfully deactivated by physical contact, such as the skin-to-skin contact, which leads to positive feelings and well-being (George and Solomon, 2016). The seek for proximity in non-threatening situations can also occur, and it strengthens the child-caregiver bond (Julius et al., 2013). The caregiver also plays other roles in this relationship, such as educator and a playmate (Cassidy, 2016).

Ainsworth et al. (1978), using the well-known Stranger Situation Test paradigm (ASST), described three styles of child attachment, largely influenced by the caregiver behavior: secure, insecure avoidant, and insecure ambivalent; a fourth style, called disorganized, was introduced by Main and Solomon (1986). According to Cassidy's (2016) deep examination of Bowlby's theory, the systems involved in the child-caregiver attachment also encompass cognitive components such as memory, selective attention, and discriminant learning, among others. Repeated cognitive and affective experiences with the attachment figure form the so-called *internal working models* (Bowlby, 1969) that can influence the way individuals will form future relationships.

ADULT AND FRIENDSHIP ATTACHMENT

Hazan and Shaver (1987) stated that, as children grow up, the attachment system does not become inactive but it is, instead, co-opted and influences the development of new bonding in adulthood. During growth, people gradually shift attachment functions from parents to peers, such as a friend or romantic partner (Fraley, 2019). In these bi-directional relationships, each person can interchangeably play the care-seeking and the caregiving roles, depending on specific situations and individual needs.

Although early caregiving experiences continue to influence the attachment orientation in adulthood (Hazan and Shaver, 1987; Chopik et al., 2014), Fraley (2019) argues that this influence can be weaker than previously thought. When two adult individuals develop an affectionate attachment, both can offer and receive support in difficult moments, each one bearing their own earlier experiences, resulting in a dynamic process of adaptation to one another. This plasticity is important for the establishment and maintainance of new relationships (Fraley, 2019), but the comprehension of how attachment patterns change during lifetime remains a challenge.

Adulthood bonding in humans is not a matter of life or death, as it is in childhood (Fraley, 2019). It seems to be driven less by biological needs and more by interpersonal needs. A friendship arises from long-term relationships that present consistency, connectedness, good communication, seeking for, and offering support to each other with high levels of trust, self-disclosure, hope, and relationship satisfaction (Welch and Houser, 2010). Friends also engage in a mutual enjoyable physical contact (Feeney and Woodhouse, 2016; Zeifman and Hazan, 2016), although to a lesser degree than in the child-caregiver dyad. Berndt (2002) noted that a high quality of friendship is characterized by high level of positive features such as pro-social behaviors and is predictive of subjective well-being (Chopik, 2017). Although a friendship usually does not cause separation distress, most theorists describe it as an attachment bond.

Seyfarth and Cheney (2012) used the term friendship to describe enduring social bonds observed in many group-living mammals, suggesting that friendship improves survival, and reproductive fitness. According to them, friendship involves cooperative interactions that can be widely separated in time, depending on memory, and emotions associated with past interactions. Intraspecific friendship is more common in individuals that are genetically related, closer in age and rank; however, it is observed between unrelated individuals (Seyfarth and Cheney, 2012).

DOG-DOG ATTACHMENT

The study of attachment bonds in dogs has focused on their relationship with humans. The presence of an intraspecific attachment bond has instead received scant attention. Studies on separation from conspecifics (Pettijohn et al., 1977; Tuber et al., 1996; Walker et al., 2014) seem to point to a difference in the nature of the social relationships dogs establish with humans and those they establish with conspecifics. Recent studies have also highlighted similarities in the relationship (not attachment) established with humans and with other dogs (Cimarelli et al., 2019).

As for intraspecific attachment, preliminary data suggest that an attachment behavioral system exists in the puppy-mother relationship (Prato-Previde et al., 2009). Although separation stress was observed in an intraspecific version of the ASST (Mariti et al., 2018), Mariti et al. (2014) did not find evidence of an attachment system in intraspecific relationships between adult dogs. In case puppies and mother keep living together in adulthood, the bond between them presents some characteristics of an attachment, more than the bond between two unrelated, co-habitant adult dogs (Mariti et al., 2017).

The use of ASST with couples of co-habitant adult dogs showed that the presence of a human stranger had a stronger ameliorative effect when compared to the presence of an older female dog living in the same household. Nonetheless, the ameliorative effect was almost identical when the stranger was compared to the canine mother (Mariti et al., 2017). The bond between adult dogs does not seem to fit all the characteristics of an attachment bond as intended in a child-caregiver or in a dog-human bond (Mariti et al., 2013). However, results should not be regarded as conclusive, considering the small number of studies on this topic and the peculiar appeal that human beings have to dogs. Such bond might be better investigated using different tools.

It must also be noticed that many factors may impact the kind of relationship dogs establish with conspecifics and the behavior dogs display in the ASST test. For instance, early weaning (Mogi et al., 2011), early separation from littermates (Pierantoni et al., 2011), the amount of maternal care received (Guardini et al., 2017), as well as disruption of the bond with tutors (Prato-Previde and Valsecchi, 2007), are all factors known to affect the development of dogs' social and emotional behaviors. At the same time, the age of the dog might influence the display of attachment-related behaviors both in intraspecific (Carlone et al., 2014) and interspecific tests (Mongillo et al., 2013).

DOG-TUTOR ATTACHMENT: A CHILD-CAREGIVER OR A FRIENDSHIP ATTACHMENT?

Dog–human dyads can establish many different kinds of relationship and bonding (Payne et al., 2015); however, when specifically studying attachment bonds, authors refer to the child-caregiver one (Rehn and Keeling, 2016).

If we compare the dog-tutor bond to the child-caregiver attachment, what would be the role, and the weight, of the attachment system, and caregiving system that the tutor and the dog carry in this relationship? Many questions arise at this point and not all can be easily answered.

The child-caregiver approach explains a good part of the dog-tutor relationship. Most decisions in the dog's life are made by the tutor, who plays the role of caregiver and provider of the dog's needs, including security. The ASST adapted to study the bond developed by the dog toward the tutor has been widely used and has repeatedly shown that dogs behave similarly to children in a stressful situation, seeking for the proximity of their tutors, preferring them to an unfamiliar person and exploring their surroundings more when tutors are present (e.g., see Topál et al., 1998; Palmer and Custance, 2008; Mongillo et al., 2013; Mariti et al., 2018; Carlone et al., 2019). Both the secure base (Mariti et al., 2013) and the safe haven effect (Gácsi et al., 2013) have been observed in the dog-tutor bond. Preliminary data also suggest that dogs tested in the ASST with their tutors present similar attachment styles as children (Solomon et al., 2019).

However, the dog-tutor relationship is a more complex phenomenon. For almost their lifetime together tutor and dog are adult individuals, from different species. The well-distinguished roles of the child and caregiver are not fixed in the dog-tutor attachment. The relationship is less asymmetrical and more reciprocal than the child-caregiver bond. Dogs can also represent an attachment figure for people. Separation from the dog can trigger anxiety and anguish in the tutor (Zilcha-Mano et al., 2011), while the close presence of the dog makes the tutor more confident in thinking about future goals and how to accomplish them (Zilcha-Mano et al., 2012). Sometimes the dog represents comfort and emotional support to the tutor in moments of distress (Zasloff, 1996; Dwyer et al., 2006). In this sense dogs also play a role like a secure base and safe haven for the tutor.

We can hypothesize that dogs, as humans, can carry both attachment and caregiving systems into their adult lifetime. Based on the literature, we suggest that dogs may have: an attachment system, activated by emotional stressful situations and deactivated by the proximity/contact with their tutor; and a caregiving system, activated by the dog's perception of distress or danger surrounding the tutor and deactivated by the tutor's signals of recovered well-being. Skills such as emotion recognition (Albuquerque et al., 2016) and empathy (Custance and Mayer, 2012) toward humans have already been recognized in dogs. This empathic ability motivates prosocial and helping behaviors, as demonstrated in studies in which dogs rescued their tutors from a distressful situation (Sanford et al., 2018; Carballo et al., 2020; Van Bourg et al., 2020). These evidences reinforce the plausibility of the hypothesis that dogs can also carry a type of caregiving system, but more studies are needed to better investigate the role of caregiver in dogs.

On one hand, the friendship attachment theory seems to partially explain the dynamic process of adaptation of dog and tutor to one another, combining two strategies of offering and receiving support in difficult moments. From the human's point of view, a relationship with a dog appears to be driven by interpersonal needs, a search for a long-term relationships with consistency, connectedness and closeness (Kurdek, 2009), which also resembles what a friendship offers for people (Welch and Houser, 2010; Chopik, 2017). From the adult dog's perspective, the relationship with a human is not a matter of life or death, stray dogs, for example, survive. Then, dogs also have different motivations than children to develop an attachment to their tutors, and they have a notably appeal for relationships with humans (Lazzaroni et al., 2020).

On the other hand, the child-caregiver attachment theory remains important in explaining the frequent and intense body contact between tutor and dog. The skin-to-skin contact triggers oxytocin release (see Julius et al., 2013, for a deeper discussion), the increase of which has also been demonstrated in affiliative interactions between dogs and humans (Nagasawa et al., 2009, 2015; Handlin et al., 2011, 2012). This important aspect makes the interspecific bond similar to the child-caregiver attachment.

Although along this opinion piece we focused our analyses in the relationship between an adult dog and an adult tutor, it must be noticed that, when they are puppies, dogs have the opportunity to establish a young-caregiver attachment bond, which adds even more complexity to this discussion, since it can involve a mother and/or a human caregiver (Prato-Previde et al., 2009; Mariti et al., 2020).

For social species, natural selection would have favored individuals who are motivated to form long-term bonds, not exclusively with kin (Seyfarth and Cheney, 2012). The dog-tutor attachment represents a strong, long-term bond that goes beyond the species. Whether the dog is the tutor's child or the best friend, or both, this attachment bond may be adaptative for both species and thus requires further research to be better understood.

CONCLUSIONS

Several arguments support that the dog-tutor relationship comprises characteristics of different types of attachment bonds. We suggest that child-caregiver attachment is not enough to characterize this interspecific bond and that a more integrative theory, that combines child-caregiver and friendship attachment should be considered. For example, while investigating dog-tutor attachment, questionnaires could include characteristics usually present in adult friendship; and behavioral tests could include situations aimed at triggering the caregiving system in dogs, to analyze how dogs offer support for their tutors. By suggesting that dog-tutor attachment integrates characteristics of different kinds of attachment bonds, we hope to provide a better picture of a bond that is one of the most important interspecific affectionate relationships for both species, and which appears to be much more complex than previously considered, a complexity that can be attribute to both parties.

AUTHOR CONTRIBUTIONS

CS and CM equally contributed to this opinion manuscript. Both authors reviewed and gave final approval for publication.

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ORIGINAL RESEARCH
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Human Expressions of Object Preference Affect Dogs' Perceptual Focus, but Not Their Action Choices

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Inspired by work on infants, we investigated whether dogs' behaviors are guided by human displays of preference, contrasting with the animals' own choices. In a rewarded fetching task, dogs override their own interest toward "disgusting" objects and retrieve what the owner prefers. However, in previous research, both objects were inherently neutral to the dogs and they might have chosen the owner's object because a "happy owner" predicts a positive outcome. If dogs are indeed able to override their own interests, we expected them to fetch the owner's object even if (1) they would prefer another one and (2) do not receive a reward for it. Two objects were compared, a toy (hoop) and a bracelet. After establishing that the toy was preferred by all dogs in an initial test of preference, we applied a two-choice procedure to test if either fetching or looking at the objects from a distance would be affected by the owner's choice. In Study 1, the owner demonstrated happiness toward the bracelet and disgust toward the toy with both facial and body gestures accompanied by verbalizations. Then the owner asked the dog to fetch, without providing additional guiding cues. All dogs fetched the toy, indicating that their own choice was not overcome by the positive emotional state signaled by the owner. To avoid direct contact with the objects, in Study 2 we placed the objects on an unreachable spot after the emotion demonstration and measured the duration of looking at the objects. In the "bracelet" (non-matching) group the owners demonstrated happiness toward the bracelet and disgust toward the toy, similar to Study 1. In the "toy" (matching) group the owners showed happiness toward the toy and disgust toward the bracelet. When the objects were placed on the unreachable spot, dogs looked at both objects for the same amount of time in the non-matching group, but longer at the toy in the matching group. Although the studies did not demonstrate that dogs override their own preferences for an object, the results suggested that the owners' expressed preference was perceived by the dogs and guided their perceptual focus.

Keywords: emotion recognition, desire state attribution, object choice test, disgust, dog

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INTRODUCTION

Studies on the cognitive and emotional development of pre-verbal children often face similar challenges as those conducted with non-human animals. Inspired by work on infants (Repacholi and Gopnik, 1997) we decided to test dogs' ability to use human emotional expressions as an informative cue in a two-choice task in which the dogs' own preferences for the options competed with the expressions humans made toward the choices. Repacholi and Gopnik (1997) investigated whether human infants understand subjectivity of the desire, i.e., that different people can have different attitudes toward the same object. They used two types of food (cracker and broccoli) and created two groups. These groups differed in terms of which food the experimenter desired, with the underlying assumption that participants would exhibit a strong preference for one food (cracker). The results indicated that 18-month-old children offered the food to the experimenter, which she previously preferred, even in cases when the children did not prefer this particular food (broccoli). In contrast, 14-month-old children offered the crackers (i.e., the food they preferred), regardless of the experimenter's preference display. Based on the results, the authors suggested that 18-month-olds can infer other's preferences and they recognize how desire can be inferred from emotional expressions.

We hypothesized that similar to infants, companion dogs' behavior might also be influenced by expressions signaling the owner's desire, even if it is in contrast to their own. Several studies provided evidence that dogs are able to discriminate between human facial expressions. Nagasawa et al. (2011) tested the ability of dogs to discriminate blank from smiling faces of their owner in a two-object choice task and whether the sensory learning would generalize to novel pictures, including those of unfamiliar people. Dogs were also shown to be sensitive to ostensive cues (Tauzin et al., 2015) or, in case of the old cohort, human voices with different valence (Smit et al., 2019). In two-object choice tasks, dogs chose objects which were attended to humans with facial expressions signaling preference (Prato-Previde et al., 2008; Buttelmann and Tomasello, 2013; Merola et al., 2014; Turcsán et al., 2015). However, as these studies used neutral stimuli for the dogs (e.g., identical plastic bottles for both the positive and the negative situation in Turcsán et al., 2015), it is unclear whether dogs are able to differentiate between their own preference and that of the owner. A study by Prato-Previde et al. (2008) used a contrast between the owner's preference expressed for two quantities of food and the dogs' inherent preference for the larger amount, but the effect of the owners' expressed preference was strongest when quantity information was removed by offering two equally small amounts.

Importantly, information about others' internal states (e.g., preference) might be utilized differently between species, leading to differences in which behaviors are affected. In comparisons between human children and young chimpanzees (Warneken, 2006) behaviors indicative of altruistic motives or prosocial helping are more strongly expressed in human children. Although dog social cognition appears to have adapted to the human social environment (Hare and Tomasello, 2005; Topál et al., 2009) there is also evidence accumulating that dogs can be more competitive and/or less prosocial compared to their closest wild relative – the wolf (Range and Virányi, 2014; Dale et al., 2017, 2019, 2020).

Not only prosociality but also inhibitory control (the ability to overcome an immediately rewarding behavior in favor of a delayed and ultimately more rewarding one) affects social decision making, i.e., the extent of how goal-directed behaviors are affected by others' preference (Macphail, 1970; Hulbert and Anderson, 2008; Bari and Robbins, 2013). In other words, actively helpful behavior might require the suppression of one's own preference in addition to being able to perceive what others want. In children, self-control can inhibit the impulse to act selfishly as altruistic 4–6-year-old children perform better on an inhibition task than non-altruistic children do (Aguilar-Pardo et al., 2013). Dogs also vary in impulse control demonstrated in a touch screen test (Bunford et al., 2019), but a link between inhibitory control and social behavior was found so far only for the expression of inequity aversion, which is stronger in dogs with higher inhibitory control (Brucks et al., 2017), but not for cooperative behaviors (Dale et al., 2020). The capacity to inhibit prepotent responses can vary significantly even between taxa (linked to the maturity of the dorsolateral prefrontal cortex), e.g., capuchins (*Cebus apella*) easily inhibit the tendency to reach directly for food but tamarins (*Saguinus oedipus*) do not, despite extensive training (Lakshminarayanan and Santos, 2009). Importantly, we expect inhibition to play a role in how animals react to communicative signals, even if emotional expressions are not received as information about internal states. Expected rewards associated with a satisfied human may compete with rewards deriving from own preferences, in which case being able to choose the former over the latter may also require inhibitory control.

In light of this literature, we consider here that sensitivity for others' internal states, like preference, might not necessarily show up in active behaviors. Dogs may lack the self-control to overcome contact with their preferred object and therefore we will test not only fetching but also looking orientation when the objects are unreachable. We assume that the owner's preference expression might causally impact dogs' behavior. The latter, looking duration and orientation, has been shown on several occasions to reflect a relocation of attention/interest in dogs (Miklósi et al., 2003; Bognár et al., 2018; Petrazzini et al., 2020) and possibly also to signal communicative intent (Miklósi et al., 2000). Given that actively helpful behaviors, like offering (Repacholi and Gopnik, 1997), might be strongest in human children (Warneken, 2006) we expect that the perceived preference of others might be less influential on behaviors like fetching, and more visible in measures of looking time as an operationalization of perceptual focus in dogs. The influence of human preferential expressions is also expected weaker in the fetching condition if we assume that the underlying driving force of dogs' behavior is a competition between social and non-social rewards. Objects in reach qualify as strong affordances (Gibson, 1977) and might distract from socially cued rewards.

The present study is a direct follow-up of research Turcsán et al. (2015), where the authors claimed that "dogs are able to recognize which is the more positive among two emotions, and in a fetching task situation, they override their own interest in the 'disgusting' object and retrieve what the owner prefers." However, overriding their interest was "easy" for the dogs in the cited study, as the two objects (plastic bottles) were originally neutral for the dogs and they could simply choose the positively marked object upon request because a "happy owner" predicts a positive outcome. In order to investigate whether dogs indeed link the owner's emotional expression with his/her internal state and not with the associated reward, the valence difference between objects in the two-choice paradigm has to be different from each perspective: one should be more attractive for the owner, and the other more attractive for the dog. We expect that if dogs are indeed able to override their own interest, they will fetch the owner's object even if they would prefer another one and they do not receive a reward for it. Therefore, (1) we used two objects with different inherent valence, one clearly preferred by the dogs and (2) we have not rewarded the dogs for their choice, contrary to previous studies when the choice of objects marked by the positive emotional expression of the owner resulted in food (Buttelmann and Tomasello, 2013; Turcsán et al., 2015) or toy rewards (Merola et al., 2014), which may have affected the choice behaviors of the subjects.

Although in the study of Repacholi and Gopnik (1997) it was the experimenter who demonstrated emotions, we asked owners to fulfill this task. In spite of possible limitations (owners are not professional actors), previous work has shown that dogs distinguish better between positive and negative emotional expression of their own owners compared with an unfamiliar experimenter (Merola et al., 2014).

To sum up, our main goal was to investigate whether dogs' behaviors are guided by human displays of preference, contrasting with the animals' own choices. How information about preference is exactly transmitted and what it means to the receiver is outside the scope of the present work, however. Note, that in externally observable behaviors, mechanisms like empathy or communication cannot always be distinguished (Miklósi, 2009).

GENERAL METHODS

Ethical Statement

The behavioral observations conducted in this study complied with national (Hungarian law: "1998. évi XXVIII. Törvény" 3.§/9. – The Animal Protection Act) and EU legislation, as well as institutional guidelines. The Hungarian "Animal Experiments Scientific and Ethical Committee" approved the experimental procedures under the numbers: PE/EA/2019-5/2017. Owners provided written consent to their participation. Our Consent Form was based on the Ethical Codex of the Hungarian Psychologists (2004). We took special care to ensure that the consent process was understood completely by the participant. In the Consent Form participants are informed about the identity of the researchers, the aim, procedure, location, expected time commitment of the experiment, the handling of personal and research data, and data reuse. The information included the participant's right to withdraw their consent at any time. Participants could easily (and without penalty) decline to participate and could ask not to use or delete data collected during the experiments.

Location and Setup

The tests took place in a 5 × 2.5 m room. Only the dog, the owner, the experimenter, and a chair were present in the room. There were markings on the floor indicating the locations of the objects (1.5 m apart from each other and 2.5 m apart from the subjects' starting place) and also a chair for the owner (**Figures 1A–D**).

The experimental objects were two objects, a toy, and a bracelet. The toy was a green, flexible rubber ring (a hoop), 9 cm in diameter, the bracelet was a black plastic ring with purple flower-patterned textile cover, 7.5 cm in diameter (**Figure 1E**). The objects were cleaned after each test.

The tests were video-recorded from the time-point when the dog entered until it left the room and used later for behavior coding. Dogs were free to explore the room for 5–6 min before the trials, while the experimenter was instructing the owner. After a few minutes, the dogs were standing/sitting/lying passively, suggesting that the habituation period was long enough to decrease potential stress due to the new situation.

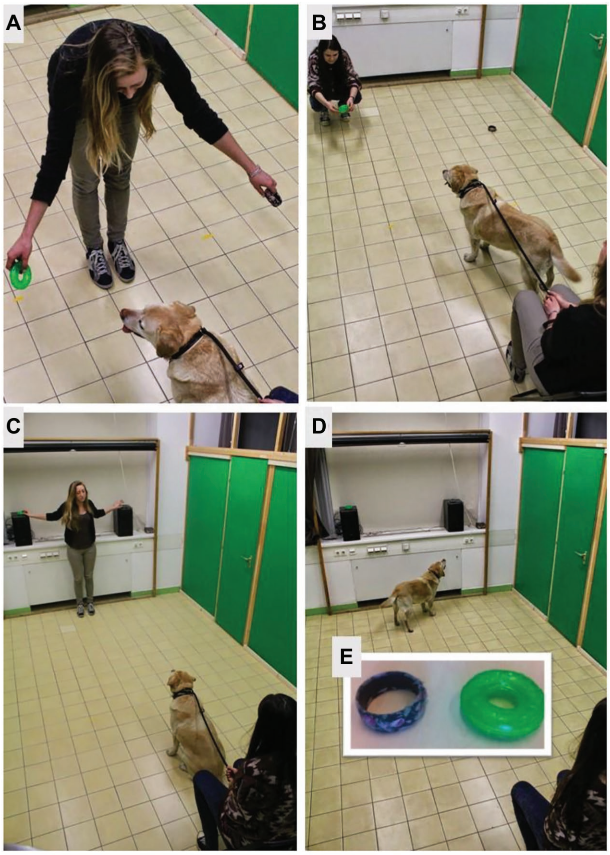

FIGURE 1 | (A) Object preference test, **(B)** demonstration by the owner, **(C)** object hiding in Study 2, **(D)** looking at the objects in Study 2, **(E)** test objects for all dogs: bracelet (left), toy (right), both 9 cm in diameter. The persons identifiable in the images provided written consent for the publication.

Dogs were recruited on a voluntary basis from the Family Dog Project database in Budapest, Hungary. Only those dogs that knew the "fetch" command (in Hungarian) according to their owners were included.

STUDY 1: FETCHING OBJECTS

We investigated whether dogs make choices based on the owners' preference, and therefore fetch the object, which is associated with their owner's positive emotional expression, despite their own preference to the contrary.

Subjects

Twelve dogs (eight mixed-breeds, border collie, golden retriever, Labrador retriever, dachshund, mean age +/− SD = 3.80 +/− 1.17 years, age range: 1.5–8.5 years, five males, seven females) were studied.

Object Preference Test

We observed which object was preferred by the dog. The owner sat down on the chair and held the dog on a leash. In front of them, the experimenter showed the two objects to the dogs (i.e., put both objects in front of the dogs' nose) for 3–4 s. One object was held in the right hand, the other in the left (randomly). After the dog smelled both objects, the experimenter opened her arms (**Figure 1A**). The dog was free to move toward the objects. If the dog tried to grab the object, the experimenter took it away and after a few seconds, she opened her arms holding the objects again. We observed which object was followed by the dog. If the choice was unclear because the dog has not followed either object, the trial was repeated. After a clear choice (i.e., the dog oriented toward/touched one object continuously for at least 5 s), the experimenter gave the objects to the owner, took the leash of the dog, and instructed the owner about the setup of the following demonstration phase (starting side and the order of the emotions).

Demonstration by the Owner

After the object preference test, the owner stood up, showed both objects in front of the dog, then backed 3 m, and put down the objects 2 m away from each other. Then s/he crouched down behind one object, touched it, looked at the dog, and gave the instructed emotional expression (happy for the bracelet and disgust for the toy) for 3–4 s (**Figure 1B**). Concerning the demonstration, we followed the protocol of Turcsán et al. (2015). The owners displayed both facial and body gestures accompanied by verbalizations. The owners were instructed that they should try to display these emotions as they usually do, e.g., when they try to invite the dog to play or when their dog found something particularly distasteful. They were not allowed to use any word known as a command for the dog during the demonstration.

Then the owner put the object back in its place, walked to the other object, and repeated this display with the other assigned emotion. During the demonstration, the experimenter stood silently behind the dog, looking toward a point halfway between the objects. After the demonstration, the owner left the objects on the floor, walked back to the chair, sat down, grabbed the leash, and positioned the dog in the middle, facing toward the objects.

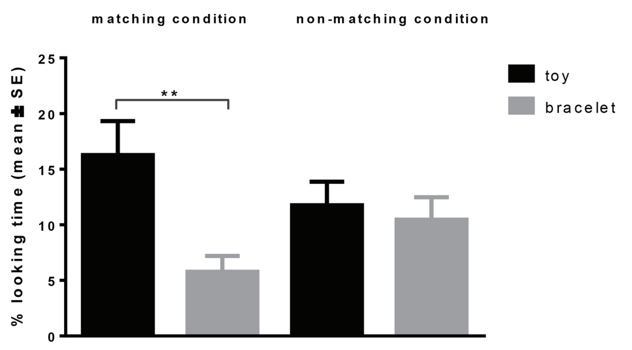

FIGURE 2 | Duration of looking time (in percent) at the toy and the bracelet in the matching (owner reacts happy toward toy, with disgust toward bracelet) and non-matching (owner reacts happy toward bracelet, with disgust toward toy) condition in Study 2. Significant differences are indicated ($^{**}p < 0.01$).

Fetching

The owner released the dog and immediately gave the "Hozd" verbal command ("Fetch" in Hungarian). The owner was strictly instructed not to use any gestures or directional cues and they were required to look straight ahead between the objects while giving the command. If the dog started to move toward the objects, the owner stopped talking and sat silently and motionless. After the dog fetched one of the objects to the owner, the dog was briefly praised by the owner. During this phase the experimenter stood silently next to the owner, looking at a point halfway between the objects. The maximum duration of the fetching phase was 1 min. Next, the experimenter retrieved both objects, and the next trial started with the Demonstration phase.

Each dog received four trials, the side of the objects and the direction of the demonstration (from left to right or vice versa) changed randomly in every trial. We recorded whether the dog fetched the toy or the bracelet during the fetching of an object phase.

Statistical Analysis

We used only descriptive statistics in Study 1. The behavior of eight dogs were coded by a second observer. The two observers agreed fully regarding both the object preference and the fetched object variable.

Results and Short Discussion

In the object preference tests, all dogs chose the toy. In the fetching test all dogs fetched an object at least in one trial: one dog in one trial, four dogs in three trials, and seven dogs in all four trials. From the altogether 41 fetching events, the bracelet, that was preferred by the owner during the demonstration phase, was fetched only 2 times (5%) by two dogs (one dog fetched the bracelet in the second, the other in the fourth trial). Therefore, dogs fetched the object which was preferred by them (the toy), and not the object that which was preferred by the owner. Thus dogs either (1) are not able to distinguish between their and the owners' preference based on his/her happy emotions toward the bracelet or (2) their own preference has not been overwritten by the positive emotional state signaled by the owner (i.e., they did not inhibit the "wrong" response; Bari and Robbins, 2013). The second interpretation can alternatively concern a competition between rewards associated with the toy and with a happy owner, but in both variants we assume that acting upon the toy was not suppressed in favor of acting upon the owner's social referencing. Moreover, we assumed that an object in reach acts as a stronger affordance (see Gibson, 1977), while previous work also had shown that objects out of reach stimulate what appears to be "showing" behavior in dogs (Miklósi et al., 2000) suggesting that placing the objects out of reach could stimulate dogs to direct more attention toward their owners, thereby also weakening the affordance provided by their preferred object. To test the second hypothesis, we decided to put the objects at unreachable positions, thereby preventing direct contact, which likely decreases the play drive. We assumed that the time spent looking at the toy or bracelet would reflect the owner's expressed preference. In particular, we expected the longest looking duration for the object preferred by both dog and owner and the shortest for the object disliked by both. Thus, a significant difference between time spent looking at the toy and bracelet was expected in the matching condition (owner expressing a preference for the toy).

STUDY 2: LOOKING AT THE OBJECTS

In this study, both objects were placed out of reach when the owner was asking for them and this way we could compare looking time and orientation between two groups of dogs: one with owners who preferred the same object as the dog (the toy), and one with owners who preferred the other object than the dog (the bracelet). We expected the greatest difference in looking times between the two objects in the matching condition (preference expressed for the toy, but disgust toward the bracelet), while in the non-matching condition looking times should differ less as a result of interference between own and other's perceived/inferred preference.

Subjects

Fifty one dogs, naïve to the procedure of the previous study, were assigned to two groups.

In the matching condition (Toy group) 26 dogs participated (1–10 years old, mean age = 3.55, SD = 2.23 years, 50% males, 58% neutered, eight mixed breed dogs, three golden retrievers, two English bullterriers, two Staffordshire bullterriers, two beagles, Labrador retriever, English cocker spaniel, whippet, miniature schnauzer, great Dane, pumi, Cavalier King Charles spaniel, labradoodle, border collie).

In the non-matching condition (Bracelet group) 25 dogs were involved (1.3–8.5 years old, mean age = 3.89, SD = 2.14, 44% males, 72% neutered, 13 mixed breed dogs, two golden retrievers, three Labrador retrievers, border collie, miniature dachshund, Airdale terrier, bichon Havanese, standard poodle, Transylvanian hound, beagle).

Object Preference Test

The test was the same as in Study 1.

Demonstration by the Owner

In the matching condition (toy group), the owner displayed happiness toward the toy and disgust for the bracelet. In the non-matching condition (bracelet group), s/he displayed happiness toward the bracelet and disgust for the toy. Otherwise the procedure was the same as described in Study 1.

Object Hiding

After the demonstration, the owner went back to the dog, sat down on the chair, and held the dog on a leash. The experimenter went to the objects, put both objects on the window sill 2 m apart from each other (**Figure 1C**), out of reach from the dog, and went back next to the chair.

Object Requesting

The owner let the dogs free and said "Hozd" to the dog ("Fetch" in Hungarian). Owner was instructed not to use any directional cues and look directly ahead. The dog was free to move in the room and could see the objects but could not reach them. The length of the phase was 30 s (**Figure 1D**). Duration of "looking at the bracelet" and "looking at the toy" behavioral variables were measured (as %, by dividing them with the total time of this phase).

Statistical Analysis

The variables were coded by a second observer for eight subjects. We evaluated the inter-observer reliability using two-way random intraclass correlation (ICC, McGraw and Wong, 1996), looking for absolute agreement between average measures. ICC was 0.706 for looking at the bracelet and 0.764 for the looking at the toy variable. During the looking at the object test three dogs did not look at any objects (one dog from the toy, two dogs from the bracelet group); these dogs were excluded from further analysis. four dogs (two from both groups) had to be excluded because of technical issues (problems with following the protocol). Therefore, the final sample sizes consisted of 23 dogs in the toy and 21 dogs in the bracelet group.

A generalized linear mixed model (GLMM) was used to investigate how looking duration differed between objects and conditions. In particular, the initial model included the predictors age, sex, reproductive status, condition (2 levels: matching vs. non-matching) and object (2 levels: toy vs. bracelet), as well as the interactions sex × reproductive status and condition × object. A model with a Gamma distribution assumption (Nelder and Wedderburn, 1972), a robust test of coefficients and a Satterthwaite method for calculating the degrees of freedom was specified, since the assumption of normal distribution was violated (Kolmogorov-Smirnov test of normality for the residuals of looking duration, $p < 0.001$). The model was optimized by backwards elimination combined with an Akaike information criterion, i.e., the least significant predictors that were not part of an interaction were removed until an optimal (smallest) Akaike value was reached. Prior (control) and post-hoc analyses consisted of *t*-tests (paired *t*-tests for within condition comparisons and independent samples *t*-tests for between condition comparisons). All analyses were conducted in SPSS v25.

Results and Discussion

Condition had no effect on the total proportion of time spent looking at either object (independent samples $t = -0.037$, $p = 0.971$), i.e., on average dogs in each condition spent 22% of the time looking at any object (either toy or bracelet).

The final model predicting looking duration (% of total trial time) included the factors condition, object, and their interaction. The interaction condition × object was significant (GLMM, $F_{1,80} = 4.585$, $p = 0.035$). Dogs looked longer at the toy than the bracelet in the matching condition (16.3 ± 3 vs. 6.3 ± 1.5, % looking duration, means ± SE; $t_{80} = 2.986$, $p = 0.004$, **Figure 2**), but not in the non-matching condition ($p = 0.636$). Between conditions, there was a trend for longer looking times directed at the bracelet in the non-matching condition (11 ± 2 vs. 6.3 ± 1.5, % looking duration, means ± SE; $t_{80} = 1.878$, $p = 0.064$). No difference was found between conditions for looking duration toward the toy ($p = 0.285$).

The demonstration of the owners affected the dogs' behavior. If the preference of the owner and the dog matched, dogs looked more at the preferred object (the toy) than the non-preferred (bracelet). If the preference did not match between the dog and the owner, the time of looking at the object which was preferred by the owner, but not the dog (i.e., the bracelet), showed a trend to increase. The result suggests that dogs' looking behavior is influenced by an interaction between the preference of the owner and their own preference. In particular, the pattern observed between conditions implies that dogs' own preference and aversion were amplified if matching with the owner's demonstration since a difference in time spent looking at each was significant only in the matching condition.

It is not certain from these results, however, if the emotional expression or the orientation of the owner's gaze were the relevant key stimulus. Therefore, in a further study, we investigated whether the owner's gaze during the object requesting phase is indicative for the dogs during the object choice phase.

STUDY 3: THE EFFECT OF DIRECTED GAZE

With this study, we investigated the "Clever Hans effect," i.e., whether owners guide their dogs with minor clues, unnoticeable to the human observer. Therefore. here, we tested whether dogs follow a major clue, i.e., directed gaze. If not, most probably they do not follow minor clues either.

We asked owners during object requesting to directly look either to the object positioned at the right or the left (identical pots were placed in both locations) and investigated whether the dogs' looking behavior is linked to the gazing direction of the owner.

Subjects

Eleven dogs, naïve to the procedures of the previous studies, participated in this test (mean age = 4.95, SD = 3.15 years, 54.5% males, 27.3% neutered, three mixed breeds, two German shepherd dogs, 1-1 Labrador retriever, Parson Russel terrier, Yorkshire terrier, sheltie, whippet, Pembroke welsh corgie).

Training

The dogs were trained to search and fetch a dog toy from a brown, non-transparent flower pot. The owner sat on the chair and asked the dog to sit in front of him/her, facing toward the experimenter who stood in front of them. The experimenter put a pot in front of the dog on the floor, showed the toy to the dog and then put it into the pot. The owner asked to fetch the toy then she gave the toy back to the experimenter. The training trial was repeated twice, with the pot positioned 1 meter from the starting position on trial 1 and 2 m on trial 2.

Object Hiding

The experimenter asked the owner to put the dog on the leash and sit on the chair. Then she put the toy in her pocket with her back to the dog so the dog could not witness this procedure. Then she put two identical, empty pots on the window sill 2 m apart from each other, out of reach of the dog, and went back to the starting place, similarly to Study 2.

Object Requesting

This phase was similar to Study 2 save for the owner was instructed to look at one of the pots during the test phase; the direction was balanced between the owners.

Results and Discussion

In the object requesting test, dogs did not look significantly more or less at the pot which was being watched by the owner (pot watched by the owner: 11.67 ± 2.63 vs. pot did not watch by the owner: 17.23 ± 4.05%, means ± SE; paired $t = 1.039$, $p = 0.323$). The looking direction of the owners during the test did not influence the dogs' choice.

GENERAL DISCUSSION

Our study aimed to investigate how dogs choose between two different objects if one (a toy) was more attractive to them, but their owner displayed preference for another object (a bracelet). In Study 1, we found that dogs did not fetch the object, which was more attractive for the owner more often. However, when the objects were at an unreachable position in Study 2, dogs' looking orientation was aligned more strongly with their own preference if the owners' expressed preference was matching. The interaction between condition and object in Study 2, as well as a trend for increased looking toward the less preferred bracelet in the non-matching condition, suggest that looking times, but not fetching, were influenced by the owner's expression of preference, but not with his/her potential directional gaze during the object request phase.

It is not certain that this influence is the result of inferred and shared representations (as in Meltzoff's "Like Me" hypothesis; Meltzoff, 2005), since in theory, human emotional expressions could also act as sign stimuli that induce attentional modulation directly, without intermediate cognitive processing. The emotional cues may, for example, act as local enhancers to guide the dogs' attention (Arbilly and Laland, 2014). The fact that preference demonstration (by the owner) and measures of looking responses were not simultaneous, argues against the objects being enhanced in a way similar to what is seen in local enhancement, however. Indeed, social referencing has been associated before with effects lasting beyond immediate demonstration (Fugazza et al., 2018) and thus the underlying process must be regarded as more complex. Another reason to exclude simple stimulus enhancement is that an expression was demonstrated toward both objects, thus the underlying mechanism is sensitive to the valence of the referential expression. Considering that dogs seem better at distinguishing strongly opposing emotional expressions from each other than emotional vs. neutral expressions (Nagasawa et al., 2011), it is crucial that in Study 3 neutral gazing alone did not influence the looking direction of the animals.

Comparison with the study by Repacholi and Gopnik (1997), conducted in 14- and 18-month-old children, is somewhat limited since the children's understanding of others' desires was operationalized by their offering behavior. It can be assumed, as proposed here, that fetching is a functional equivalent in dogs, but this relies on further assumptions about the underlying cognition of the behavior (e.g., that dogs understand fetching as an act of offering an object to a human). Since only looking behavior was influenced here by the owner's preference in Study 2, it is possible that response inhibition, an important aspect of cognitive control (Macphail, 1970; Hulbert and Anderson, 2008; Bari and Robbins, 2013), was not sufficiently strong to overwrite the animals' own preference in Study 1. Dogs' ability to inhibit their behavior is considered a hallmark of domestication (Hare and Tomasello, 2005; Hare et al., 2012), but differences to wolves regarding this capacity vary based on the type of task (Marshall-Pescini et al., 2015; Brucks et al., 2019) and exhibit a wide variation between individual animals (Brucks et al., 2017). Its relationship to social cognition and behavior is also not uniform and appears more relevant for the expression of inequity aversion (Brucks et al., 2017) than cooperation (Dale et al., 2020). Weaker inhibition as a possible explanation will need to be demonstrated more directly in the future. Interestingly, freeing the owner from a closed space is an active behavior more likely (than fetching) to align with the owner's expressed emotion (Carballo et al., 2020; Van Bourg et al., 2020). Our results suggest that in the above studies, the dogs' interest to remain close to the owner (Topál et al., 1998) and the owner's display of distress might enhance one another, since we also observed a stronger alignment between dogs' preference and looking orientation, if it was matching with the owner's expressions.

Other reasons that dogs' fetching behavior in this study does not match with the offering behaviors of infants (Repacholi and Gopnik, 1997) might relate to uniquely human aspects of early prosocial development. Human infants display signs of altruistic sharing and fairness concern surprisingly early (as young as 15 months; Schmidt and Sommerville, 2011). Although the extent and limitations of early human altruism are still debated (Wynn et al., 2018), it seems stronger in human children than in young chimpanzees (Warneken and Tomasello, 2009). It is thus possible that some forms of responding to others' preferences are uniquely human. Some work additionally suggests that dogs are more competitive and less prosocial than wolves (Range and Virányi, 2014; Dale et al., 2017, 2019), which might interact with how potential capacities to be influenced by the internal states of others are expressed in measurable behavior. The latter has been demonstrated for imitation (Range and Virányi, 2014), which is less accurate in dogs compared to wolves.

Yet another limitation with using fetching to operationalize sensitivity for owner's preferences concerns the embodied nature of self-other representations, discussed with regard to imitation for children (Kee, 2020) and also dogs (Topál et al., 2006). Within this framework, it is crucial that fetching is not part of a shared motor repertoire (between humans and dogs) and hence the behavior by itself might prime a more egocentric response.

Finally, a completely non-social explanation can be applied to how dogs' responded in the fetching task (compared to the looking task). This approach is compatible with the already suggested role of inhibitory control (Macphail, 1970; Hulbert and Anderson, 2008; Bari and Robbins, 2013), but makes no assumption about (shared) internal states. In this scenario the reward from obtaining a preferred object is competing with the expected reward of a satisfied owner. Objects of preference within reach might more likely present affordances (Gibson, 1977), whereas out of reach objects signal the need to attend to potentially helpful humans (see for example, Miklósi et al., 2000). To disentangle this interpretation from hypotheses relying on social cognition and (shared) representations should guide future efforts in the same direction. One important aspect to study in the dog is whether, as in human children (Doan et al., 2015), observing two other agents expressing conflicting preferences, can affect how the animals respond to mismatch involving their own preference. Other factors to control for in the future, concern the duration of dog ownership, which was shown to affect how sensitive the animals were to their owners expressed emotions (Katayama et al., 2019).

Overall, we can conclude that the preference of the owner influenced the dogs' looking orientation, aligning with previously reported instances of social referencing (Prato-Previde et al., 2008; Turcsán et al., 2015; Fugazza et al., 2018).

The novelty of the results relates to the use of contrasting preferences between the observer (dog) and observed (owner). Although in the study of Turcsán et al. (2015) dogs' fetching behavior was influenced by their owner's preference, the dog's own preference did not play a role (as identical objects were used and the owner's preference was the only difference). Pongrácz et al. (2013) showed that a dog's choice of hidden food to be influenced by the owner, but the animals' knowledge of the preferred food's position might have played a role, as performance tilted toward the dogs' preference in later trials. Moreover, in that study the cues were not emotional expressions of preference, but distal pointing cues. While Prato-Previde et al. (2008) used expressions of preference to influence how dogs choose between quantities of food, the expressed preference of the human informants was competing with dogs' certainty of their own quantity judgments rather than their preferences. The present work, therefore, is the first to our knowledge to directly address how conflicting preferences of self and other influence the behavior of dogs and therefore deepens our understanding of the perception, social cognition, and sensitivity to emotional expressions in these animals. Future studies will need to address, however, if competing social and non-social expected rewards might present a potential alternative explanation for social interpretations of the observed behaviors.

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 Hungarian "Animal Experiments Scientific and Ethical Committee, PE/EA/2019-5/2017." Written informed consent was obtained from the individual for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

EK, FS, and ÁM: conceptualization. EK and FS: methodology. EK and II: formal analysis and visualization. EK and ÁM: resources. FS and EG: data curation. EK, FS, and EG: writing-original draft preparation. EK: supervision and funding acquisition. SF and EG: project administration. All authors contributed to the article and approved the submitted version.

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Acquisition of a Joystick-Operated Video Task by Pigs (*Sus scrofa*)

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The ability of two Panepinto micro pigs and two Yorkshire pigs (*Sus scrofa*) to acquire a joystick-operated video-game task was investigated. Subjects were trained to manipulate a joystick that controlled movement of a cursor displayed on a computer monitor. The pigs were required to move the cursor to make contact with three-, two-, or one-walled targets randomly allocated for position on the monitor, and a reward was provided if the cursor collided with a target. The video-task acquisition required conceptual understanding of the task, as well as skilled motor performance. Terminal performance revealed that all pigs were significantly above chance on first attempts to contact one-walled targets ($p < 0.05$). These results indicate that despite dexterity and visual constraints, pigs have the capacity to acquire a joystick-operated video-game task. Limitations in the joystick methodology suggest that future studies of the cognitive capacities of pigs and other domestic species may benefit from the use of touchscreens or other advanced computer-interfaced technology.

Keywords: animal cognition, pigs, animal learning, video tasks with animals, animal behavior

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INTRODUCTION

Cognitive processes, such as memory, attention, and conceptualization permit animals to demonstrate adaptive behavior in complex, dynamic environments (Wasserman, 1993). These processes have been investigated in laboratory animal species, including non-human primates, rats, and pigeons, among other species, but have yet to be fully explored in farm animals (Curtis and Stricklin, 1991; Duncan and Petherick, 1991). Over the past 2 decades, however, investigations of farm animal cognition have significantly increased, in part because of their implications for ethical obligations toward them, as well as for decisions relating to their production, care, and management (Croney et al., 2004; Mendl and Paul, 2004; Birch, 2018; Franks, 2018; Nawroth et al., 2019). Much of the existing literature on farm animal cognition has focused on the abilities of pigs (*Sus scrofa*; for reviews, see Held et al., 2002; Gieling et al., 2011; Marino and Colvin, 2015), although emerging studies have been conducted recently with horses (e.g., Brubaker and Udell, 2016), goats (Briefer et al., 2014), and sheep (Kendrick et al., 2001; Doyle et al., 2013; McBride and Morton, 2018).

Very early studies conducted by Yerkes and Coburn (1915) gave some indication of the pig's capacity for complex learning. They found that pigs could solve multiple-choice problems presented in arrays of 2–9 boxes requiring them to: (1) select the first box on the right; (2) select the second box on the left; and (3) alternate between selecting first, the box on the right, then on the left. Later studies of cognitive capacities of domestic pigs indicated that they are capable of operant learning to obtain light (Baldwin and Meese, 1977), produce additional heat for their enclosure (Curtis and Morris, 1982; Morrison et al., 1987), and acquire feed (Croney, 1999). They also are capable of spatial learning (Mendl et al., 1997; Laughlin et al., 1999), although it should be noted that disturbances occurring during cognitive tasks have been shown to impair their performance.

Additionally, pigs have also demonstrated the capacity for discrimination and reversal learning (e.g., Klopfer, 1966; Cerbulis, 1994; Maney, 1998). For example, investigation of Klopfer (1966) of the pig's ability to learn brightness, color, and spatial discriminations, as well as reversal learning, suggested that they could discriminate based on brightness and color, but only if spatial biases were not permitted to develop in response to feeding. Klopfer (1966) also reported that pigs could acquire spatial (left or right) discrimination learning as well as reversal learning. In addition, Maney (1998) documented that pigs could discriminate between the size, shape, and luminance of objects, while Cerbulis (1994) found that pigs could respond discriminatively to human verbal and gestural commands of novel action-object combinations. Further, Croney et al. (2003) found that pigs could perform visual and olfactory discriminations successfully to locate a food resource in a novel environment, while Murphy et al. (2013) reported that pigs could learn tonal discriminations. Broom et al. (2009) found that pigs could use mirror images to locate food hidden outside of their line of sight. Collectively, these results provide evidence that pigs have the capacity to learn fairly complex novel tasks, and thus might be amenable to testing using alternative paradigms for exploring their cognitive capacities.

Computerized video-game tasks have provided an innovative means of investigating animal cognition using a variety of test subjects, from primates to pigeons (Wright et al., 1988; Rumbaugh et al., 1989; Richardson et al., 1990; Rumbaugh, 1990; Spetch et al., 1992; Hopkins et al., 1996; Markham et al., 1996; Leighty and Fragaszy, 2003). These approaches permit control of the exact temporal and spatial parameters of an animal's responses, and investigators can obtain greater stimulus flexibility because of the relatively unlimited number of visual stimuli that can be generated and presented. This is especially useful for tasks that require large numbers of novel stimuli to test how an animal learns new information over time. Similarly, joystick-operated video-game tasks require the subject to use a joystick to move a cursor until it makes contact with a target on the screen (Rumbaugh et al., 1989). Two characteristics are required for successful task completion. First, the animal must have sufficient motor skills to be able to manipulate a joystick. Secondly, the animal must have the cognitive ability to learn that joystick movements control cursor movement, and that the collision of cursor and target is followed by a reward.

Video-task acquisition has also been demonstrated in a range of primates, including rhesus monkeys, baboons, gorillas, and chimpanzees (Rumbaugh et al., 1989; Richardson et al., 1990; Lincoln et al., 1994; Hopkins et al., 1996). Computerized tasks have been used to test spatial memory in pigeons (Spetch et al., 1992) and matching-to-sample in pigeons (Wright et al., 1988), as well as operant conditioning and visual discrimination in rats (Markham et al., 1996). Because computerized tasks provide a more objective means of testing some types of cognitive processing in animals, allow for a wider variety of test stimuli, and permit precise control of stimuli and recording of responses, the current study was undertaken to explore the pig's ability to acquire a joystick-operated video-game task and evaluate the usefulness of this technology for further investigations of their cognitive abilities.

MATERIALS AND METHODS

Subjects

Two Yorkshire barrows (castrated male pigs) and two Panepinto micro pig barrows served as subjects. The animals were maintained in an indoor facility on the Pennsylvania State University campus. The Yorkshire barrows (60 and 63 kg, respectively, at the beginning of the study) were both 3 months old, and housed together in an indoor pen measuring 1.83 m × 2.3 m. The Panepinto micro pigs (43 and 50 kg, respectively) were both 24 months old and also were housed together in an indoor pen measuring 1.26 m × 2.3 m. All pigs were maintained on cement floors covered with rubber stall mats. The Yorkshires were fed a balanced, fortified, corn-soy diet *ad libitum* daily. The Panepinto micro pigs were fed 1–1.5% body weight (kg) mini-pig diet (Lab mini-pig HF grower diet 5 L80, PMI Feeds Inc., St. Louis, MO). Continuous access to an operant waterer was provided for all pigs, and all subjects were maintained on a 12/12 h light/dark cycle.

Apparatus

To determine the ability of pigs to acquire a complex visuo-spatial task using a joystick, the NASA/LRC computerized test system was used (Rumbaugh et al., 1989). The experimental apparatus consisted of an IBM 386 personal computer with a 33-cm color monitor, positioned behind a transparent Lexan window, with a modified 11-cm analog joystick shaft (Flight Pro analog joystick, model SV-215), attached to a 4.5 cm diameter gear shift knob, and a Med Associates SG-601 automatic pellet reward dispenser. The apparatus was located in an elevated testing pen (0.77 m high × 2.14 m wide × 1.50 m long) that was constructed of metal gates and woven wire flooring. A ramp constructed of 0.017 m plywood measuring 1.22 m × 0.61 m (0.42 m high at top and angled at approximately 45 degrees) and a guillotine door made from 0.007 m plywood (0.84 m × 0.53 m) allowed access to the test pen (**Figure 1**).

Prior to the experiment, the focal length of the pigs was determined by lens refraction conducted by an optometrist to find the best position for the computer monitor (see Michaels, 1975). All pigs were found to be far-sighted, with each subject determined to be between +1 and +2 diopters hyperopic. To accommodate their visual limitations, the computer monitor was positioned approximately 45 cm away from the subjects' eyes when they were using the joystick.

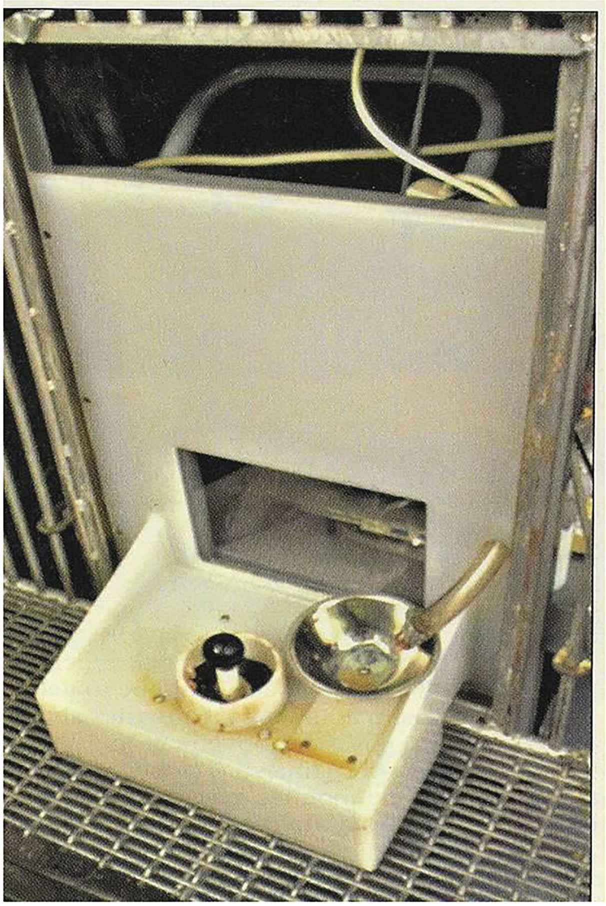

FIGURE 1 | Joystick apparatus for testing pigs.

Pre-training

A mock joystick apparatus was constructed for pre-training purposes, consisting of a black plastic gear shift knob (4.5 cm diameter) mounted on a spring, and attached to a plywood base 1.8 cm thick × 28.3 cm long × 22.5 cm wide. Sections of 10 cm PVC pipe were cut and fastened together to form a tube which delivered food rewards into a PVC cup (10 cm diameter) attached to the plywood base, approximately 10 cm from the base of the mock joystick. The pigs were shaped to approach the joystick and manipulate it with their snouts. Each time they approached the mock joystick, they were rewarded with a dog food pellet as the handler gave the command "Joystick." Eventually, the pigs were rewarded only when they approached and manipulated the joystick with a verbal command. Shaping sessions lasted approximately 10 min for each subject, and were conducted once daily, 5 days per week, until the pigs manipulated the joystick consistently on command. The mock joystick training was conducted for 2 weeks, after which the pigs reliably performed the behavior (**Figure 2**).

After the 2-week training for joystick manipulation, the pigs were shaped to watch the computer monitor when it was positioned in the experimental testing apparatus, as previously described. All subjects were tested individually, and when in position on the elevated apparatus, were given the command, "Watch the screen." When the pigs oriented toward the window in front of the computer screen, a reward was dispensed. When they were able to perform this behavior consistently, the command "Watch the screen" was paired with the command "Joystick." The pigs were reinforced immediately for attending to the computer monitor, and then manipulating the modified joystick.

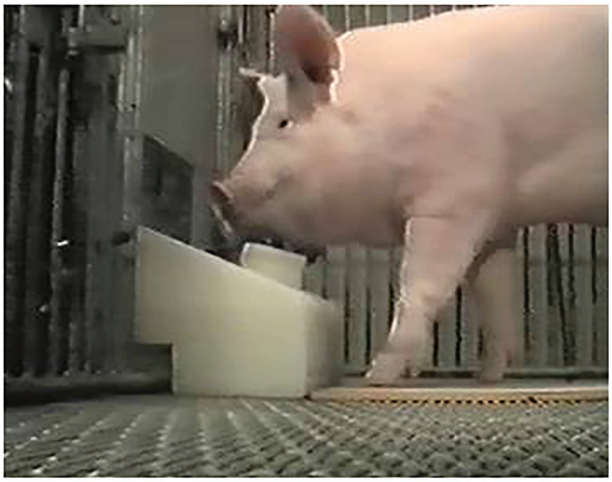

FIGURE 2 | Pig subject using joystick during testing with SIDE Task.

Side Training

After pre-training, the pigs were trained to perform a rudimentary joystick-operated video game task. The task, referred to as the SIDE task (Hopkins et al., 1996), began with a computer-generated 2.5 cm blue border around the inside edges of the computer screen which created four target walls. A white 2-cm circular cursor appeared in the center of the screen. Movement of the joystick in any direction caused the cursor to move at a rate of 8 cm/s. The pigs were trained to move the joystick to contact one of the target walls. Contact resulted in auditory feedback from a speaker (computer-generated "bloop" sound) and the delivery of a food reward (dog food pellet). An experimenter stood outside the test pen and provided the pigs with verbal and tactile reinforcement after each successful trial. Successful and unsuccessful attempts to contact target walls were recorded by the SIDE software program, and targets were randomly assigned to positions on the screen (above, below, and left or right of center). A titrated version of the SIDE task based on response latency was utilized, so that as a subject's performance improved or declined, task difficulty increased or decreased, accordingly. For example, as subjects completed a number of trials (usually five or six) within a fixed period (less than 10 s) successfully, the number of target walls was successively decreased from four target walls, to three walls, to two walls, and finally to one wall. After successful performance on the one-walled condition, the target size was successively decreased to create partial walls of different sizes (from 16 cm to 6 cm, then to 2.5 cm). Alternatively, if the subject failed to complete trials within the allotted time, the number (or size) of target walls was successively increased. Subjects were tested once daily, 5 days per week, for 12 weeks. Data were analyzed from all sessions in which pigs completed a minimum of 15 trials.

Revised Training

After approximately 4 months of training with the Panepinto micro pigs, we observed that because of the titration of the task, the pigs were completing a disproportionate number of four- and three-walled targets during sessions and were therefore making little progress on two- and one-walled targets. To correct this, the pigs were now required to complete a minimum of 15 two- and one-walled targets during each session. The Yorkshire pigs had been terminated from the experiment prior to this, and thus they were tested using only the titrated version of the task described above.

Statistical Analyses

Each subject's percentage of correct responses contacting a target wall with the first cursor movement was recorded for three-, two-, and one-walled conditions and for each of the target positions (above, below, left, and right of screen center). Because performance on four-walled targets was always 100% provided the subject completed contact, four-walled target performance was not analyzed. Performance on two- and one-walled targets was of special interest because success on these categories was more indicative of the pigs' ability to acquire the concept underlying the task, in addition to the required motor skills. Statistical analysis was performed in R version 3.6.2. Binomial testing was used to compare each subject's percentage of correct first cursor movements during their terminal performance (final block of 50) to the expected probability of success due to chance (i.e., three-walled test = 75%, two-walled test = 50%, and one-walled test = 25%).

According to Hopkins et al. (1996), in which primates' abilities to acquire the SIDE task were evaluated, criterion for demonstrating motoric skill acquisition was completion of a block of 100 trials, with at least 50% of the trials consisting of partial 1-wall targets. These investigators considered conceptual understanding of the task established when over 90% of a block of 100 trials consisted of 1-wall or partial-wall trials. At this performance level, they reasoned that the subjects understood the discriminative requirements of the SIDE task since they could move the cursor to the correct target position on a consistent basis (Hopkins et al., 1996). These are relatively strict criteria that require good dexterity by the subjects.

RESULTS

Yorkshire Pigs: Number of Target Walls

Analyses of terminal performance (last block of 50 trials) showed that neither of the Yorkshire pigs (Hamlet and Omelet) achieved significant performance on three-walled targets ($p > 0.05$; **Table 1**). On two-walled targets, both Yorkshires were above chance with 78 and 70% correct responses, respectively ($p < 0.001$). Both pigs performed above chance on one-walled targets when collapsed across target wall position (Hamlet: 48%; Omelet: 42%; $\chi^2 = p < 0.01$). The Yorkshire pigs' performance on one-walled targets over time is presented in **Figure 3**.

Target Position

Performance on the target position was analyzed for one-walled targets (see **Table 1**). Both pigs demonstrated response biases, generally performing better on vertical plane (up, down) movements than horizontal plane (right, left) movements. Hamlet was 71% correct on one-walled targets when the target was located above ($p < 0.001$), and 69% when the target was located below screen center ($p < 0.001$). Omelet was 27% ($p = 0.645$) and 69% ($p < 0.001$) correct on one-walled targets located above and below screen center, respectively.

Learning Curves

Terminal performance (last block of 50 trials) was compared to performance on the first block of 50 trials for each category of number of walls (3-, 2-, and 1-walls) and on target positions. Omelet showed no significant improvement on three- or one-walled targets over time, but did improve on two-walled targets ($p < 0.05$). Hamlet likewise improved on two-walled targets ($p < 0.025$), but not on three-walled targets. Surprisingly, his performance on three-walled targets actually declined toward the end of the experiment ($p > 0.10$). Hamlet's performance on one-walled targets also did not improve significantly.

After 12 weeks of training, Hamlet and Omelet were terminated from the experiment because they had grown too large to stand long enough to complete sessions, and also no longer fit within the constraints of the test pen.

TABLE 1 | Terminal performance of Yorkshire pigs on SIDE task.

Subject	Category	*n*	%correct responses	%Chance	χ^2	*p*
Hamlet						
	Left	10	20	25	1.30	n.s.
	Right	15	27	25	0.21	n.s.
	Above	14	71	25	112.80	****
	Below	13	69	25	103.20	****
	3-wall	50	80	75	1.33	n.s.
	2-wall	50	78	50	31.36	****
	1-wall	50	48	25	28.21	****
Omelet						
	Left	15	27	25	0.21	n.s.
	Right[a]	–	–	25	–	–
	Above	15	27	25	0.21	n.s.
	Below	16	69	25	103.00	****
	3-wall	50	74	75	0.053	n.s.
	2-wall	50	70	50	16.00	****
	1-wall	50	42	25	15.41	****

Performance on target positions (left, right, above, and below) was analyzed and presented as a function of the last 50 one-walled trials completed.

[a] Due to injury, Omelet was unable to continue training long enough to complete the minimum number of five trials in this category.

*****indicates significance at the 0.001 level.*

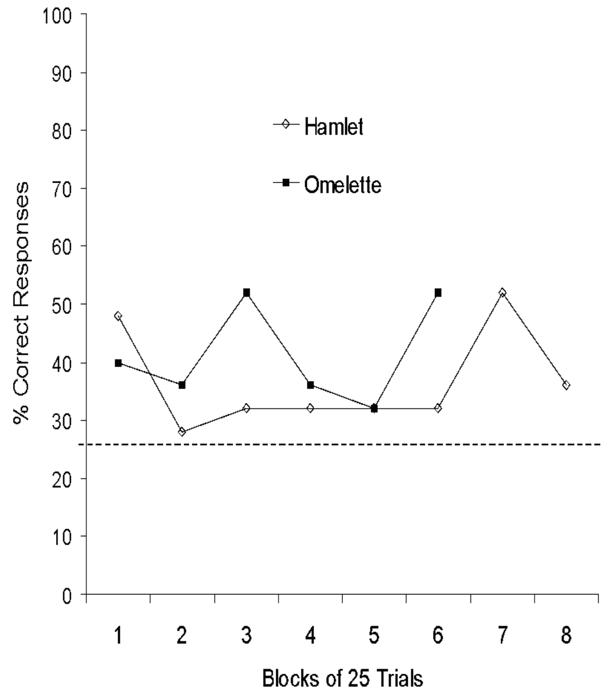

FIGURE 3 | Performance of Yorkshire pigs on one-walled targets collapsed across target position. Horizontal dashed line indicates chance performance.

Panepinto Micro Pigs: Number of Target Walls

The Panepinto micro pigs' (Ebony and Ivory) terminal performance (last block of 50 trials) was analyzed (**Table 2**).

On three-walled targets, both pigs were more successful than would be expected by chance (Ebony: 84%, $p = 0.038$; Ivory: 84%, $p = 0.038$). However, while Ivory was above chance when presented with the two-walled task (68%, $p < 0.001$), Ebony was not (56%, $p = 0.271$). Furthermore, Ebony performed only marginally better than expected by chance when presented with one-walled targets (34%, $p = 0.049$), while Ivory was 76% correct on one-walled targets ($p < 0.001$). The micro pigs' performance on one-walled targets over time is presented in **Figure 4**.

TABLE 2 | Terminal performance of Panepinto micro pigs on SIDE task.

Subject	Category	*n*	% correct responses	%Chance	χ^2	*p*
Ebony						
	Left	11	100	25	300.00	****
	Right	11	0[a]	25	33.33	****
	Above	13	61.5	25	82.12	****
	Below	15	20[a]	25	1.33	n.s.
	3-wall	50	84	75	4.32	*
	2-wall	50	56	50	1.44	n.s.
	1-wall	50	34	25	4.32	*
Ivory						
	Left	12	67	25	94.08	****
	Right	13	85	25	192.00	****
	Above	13	69	25	103.25	****
	Below	12	42	25	15.14	****
	3-wall	50	84	75	4.32	*
	2-wall	50	68	50	12.56	****
	1-wall	50	76	25	138.72	****

Performance on target positions (left, right, above, and below) was analyzed and presented as a function of the last 50 one-walled trials completed.
[a]Performance was below chance.
**indicates significance at a 95% confidence level.*
*****indicates significance at the 0.001 level.*

Target Position

The micro pigs' performance on target position was also analyzed as a function of one-walled targets (see **Table 2**). Like the Yorkshire pigs, Ebony and Ivory demonstrated response biases, particularly on one-walled targets. However, unlike the Yorkshires, they generally performed better on horizontal plane (right, left) movements than vertical plane (up, down) movements. Ebony showed a strong bias for one-walled targets positioned to the left of screen center, while Ivory's bias was for right-sided targets. Ebony's performance was significantly below chance on one-walled targets positioned to the right of the screen (0%; $p < 0.001$) and below chance when the target was located at the bottom of the screen (20%; $p = 0.292$). Ivory's performance differed from that of the other three pigs in that the disparity in his performance based on target position was relatively small. In fact, he was the only subject to perform well above chance on all positions ($p < 0.001$).

Learning Curves

The micro pigs' terminal performance (last block of 50 trials) was compared to initial performance (first block of 50 trials) for each category. Ivory's performance increased significantly for all target positions and number of walls ($p < 0.001$) except the three-walled condition. Ebony improved on targets to the left and top of the screen center ($p < 0.001$) and on three- and two-walled targets ($p < 0.05$, $p < 0.001$, respectively). After 15 months on the SIDE task, Ebony and Ivory's training was terminated.

Due to limitations of the version of SIDE task software utilized, it was not feasible to electronically extract data in a manner that would have permitted accurate, detailed analyses of error patterns for each individual. Future programming for similar or related tasks, indeed, for any species tested using advanced technology, should be sure to include the potential for such evaluation, as the error patterns observed and identified during some facets of the experiment may provide valuable information as to how information processing and physical manipulation of the joystick (or other manipulanda) subserve the animals' resulting performance.

DISCUSSION

Overall, all pigs performed significantly above chance on one-walled targets, which indicates that, to some extent, all acquired the association between the joystick and cursor movement. That the pigs achieved the level of success they did on a task that was significantly outside their normal frame

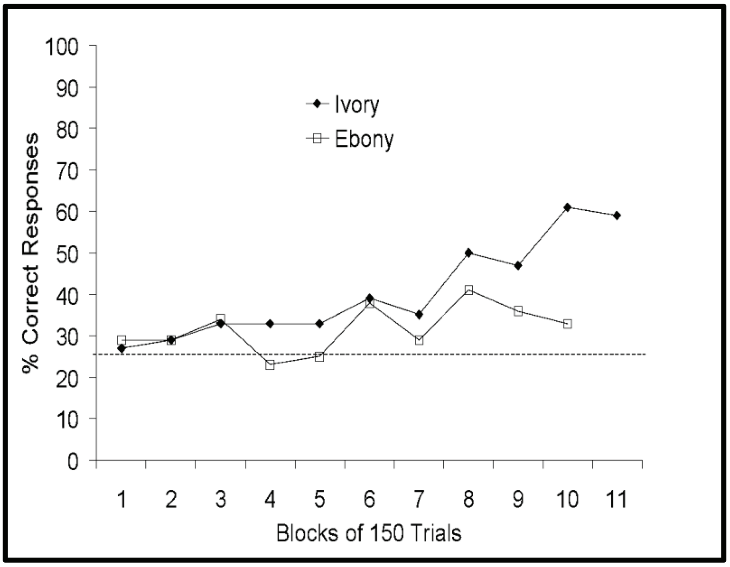

FIGURE 4 | Performance of Panepinto micro pigs on one-walled targets collapsed across the target position. Horizontal dashed line indicates chance performance.

of reference in itself remarkable, and indicative of their behavioral and cognitive flexibility. Their high level of social motivation to perform the task was also noteworthy. Although food rewards associated with the task were likely a motivating factor, the social contact the pigs experienced with their trainer also appeared to be very important. Occasionally, during some sessions, equipment failures resulted in non-reward following correct responses. On these occasions, the pigs continued to make correct responses when rewarded only with verbal and tactile reinforcement from the experimenter, who was also their primary caretaker. Additionally, during times when the task demands seemed most challenging for the pigs, and resulted in reluctance to perform, only verbal encouragement by the experimenter was effective in resuming training. This may have been due to the strong bond the pigs developed with the experimenter during training, which would support the assertion of Boysen (1992) that the human-animal bond is a crucial element in the success of animals used in studies of comparative cognition.

It should be noted that despite performing above chance on the SIDE task, even the pig that performed best did not approach the level attained by non–human primates that acquired the task after a comparable number of trials (see Hopkins et al., 1996). Indeed, none of the pigs was able to meet the criteria of Hopkins et al. (1996) for demonstrating motoric or conceptual acquisition of the SIDE task. There are several possible explanations for the pigs' failure to meet they criteria. First, they were established for dexterous primates (rhesus monkeys and chimpanzees); although no clear rationale was provided for their adoption. Thus, it was difficult to know how to adapt those criteria for pigs, taking into account their more limited perceptual and motor capabilities, which clearly differ from primates. For example, the visual demands of the task may have been particularly problematic for the pigs, since we had previously established that all four subjects were far-sighted. As sufficient visual capability is a prerequisite for successful completion of a joystick-operated-video game task, and despite attempts to position the computer monitor appropriately, it is impossible to know how well the pigs were able to see, and subsequently correctly discriminate between targets. Furthermore, because of the positioning of the pigs' eyes relative to their snouts, they were often forced to watch the screen prior to moving the joystick, and then check their progress after cursor movement was initiated. This artifact of the pigs' anatomy likely contributed to some of their errors because in order to succeed, they not only needed dexterity and conceptual understanding of the task, but perhaps also short-term or working memory (which is not well understood in pigs) of the target position locations.

In addition, the pigs' limited dexterity no doubt constrained their performance. Because the joystick-operated video-task paradigm was initially designed for use by non-human primates with great manual dexterity, modifications to the equipment were necessary so that the pigs could use their snouts to manipulate the joystick. However, the pigs' ability for such manipulation was restricted to their normal range of head and neck movements. This limitation appeared particularly troublesome for the Yorkshire pigs whose larger size also constrained their ability to reposition themselves as needed to contact targets located in the horizontal plane. Thus, it was not surprising that the Yorkshire pigs performed better on vertical plane movements, which are more frequently seen in their normal behavioral repertoire during routine activities such as rooting. In fact, when faced with left or right targets, the Yorkshire subjects were often observed to alter their stance so that they were parallel to the computer screen. This way, they could approach horizontal targets in the same way they did for those in the vertical plane. Because of their small size, the micro pigs were better able to reorient themselves as needed to view the computer monitor and complete horizontal plane movements. This flexibility likely resulted in better performance in both planes and may have contributed to their superior performance compared to the Yorkshire subjects. Ebony and Ivory's smaller size also enabled them to be maintained in the laboratory for a much longer period for training and testing (15 months) than the Yorkshire pigs. Thus, they were afforded the opportunity to continue training, thereby contributing to their improved performance on the SIDE task. Consequently, their terminal performance was much better than the Yorkshire pigs that were trained for only 10 weeks on the same task.

Additional problems that may have been attributable to dexterity limitations were observed when the pigs were unable to completely move the cursor toward a target wall and finish the trial, simply because of the angle at which the cursor approached the target. On these occasions, the pigs often nosed the joystick to move the cursor back out of the target wall and then altered the angle at which they approached the target. However, in doing so, they sometimes contacted an incorrect wall, resulting in reduced accuracy on their first cursor attempts. Further, when the pigs were unable to make contact with a horizontal target, they often resorted to strategies that allowed them to move the cursor upward, then down into the correct left or right wall. These responses were consistently observed, particularly for Hamlet and Omelet, who systematically responded with a series of movements that resembled an "inverted v" when faced with right or left targets. The resultant asymmetry in the pigs' performance relative to target position is similar to that observed in rhesus monkeys (Hopkins et al., 1996). In comparing the performance of rhesus monkeys to chimpanzees on the SIDE task, Hopkins et al. (1996) observed that the monkeys had more difficulty responding to horizontal targets, suggesting that their manipulative behavior was less diverse than chimpanzees. This problem may, in part, explain the pigs' poor performance relative to primates, as their ability to manipulate objects is significantly less dexterous and flexible.

Response biases can often be inevitable when testing animals, and they emerged during testing with the pigs as well. For example, while Ebony, like all of the subjects, showed some level of side bias (left), he did correctly move the cursor to the right numerous times on all but the one-wall task. As previously noted, these trials created the smallest targets for the pigs. Side bias training was instituted for all pigs manually upon observation of biases because although the software titrated to an easier level of task difficulty if a subject made errors consistently, the program's random generation of target locations did not facilitate training to overcome bias. This intervention was not successful, however. Learning on manual side-bias training with objects or with the joystick with the computer turned off (necessary given the previously mentioned software limitations) did not appear to generalize to the joystick-operated task. A few explanations for this observation are plausible. First, Ebony may simply have been limited in either or both dexterity and the paw/snout/eye-coordination needed to hit right-sided, one-walled targets. It is also possible that because the video-task apparatus was not centered in the pen due to constraints of the testing space, Ebony's body positioning to complete such tasks may have further constrained his performance given that additional training did not correct the side-bias problem with the joystick, although it was effective on bias correction using objects (Croney, 1999). It is also possible that some degree of instinctive drift may have impacted his and the other pigs' performance, especially as the tasks became more challenging and rewards for behaviors performed were reduced due to errors.

An alternative explanation for the difference between the pigs' and primates' performance that must be considered is that the pigs may have been unable to fully comprehend the concepts required to perform well on the SIDE task. Difficulties with the conceptual component of the task may have been due, in part, to the spatial discontiguity of the stimulus and response. Meyer et al. (1965) suggested that a primate's learning efficiency might be impaired when the hand used to execute a response was placed in an area distant from the location of the discriminative stimuli. A similar rationale may have been a factor for the pigs, since the movement of their snouts was some distance from the images displayed on the monitor, and the lateral placement of their eyes may have contributed to a cognitive disconnect between their movements and the resulting changes appearing on the screen.

In addition to the difficulties posed by limited dexterity and vision, several methodological factors may also have impeded the pigs' performance on the SIDE task. First, because a protocol for testing pigs using the joystick-operated video-game task paradigm had not previously been established, the methods used in the current experiment were exploratory. As such, some changes in procedures and equipment were necessary during the experiment to correct concerns as they emerged. For instance, early design flaws in the joystick apparatus were detected and required correction. Initially, the protective welded plastic area surrounding the joystick was too high and impeded movement of the joystick in all directions. In addition, positioning of the feed delivery tube attached to the automatic dispenser sometimes resulted in failure to deliver rewards to the pigs after correct responses early in training and required correcting. This delay in reinforcement following a correct response may have impeded the animals' initial learning. Finally, the test pen was designed so that the joystick apparatus was positioned approximately 0.04 m away from the right side of the pen. This initial positioning proved to be significant in that it restricted the pigs' abilities to stand or move to the right of the joystick.

Initial training procedures also proved to be problematic. One problem in the training process was that the pigs were allowed to work at their own pace, which resulted in a large set of data consisting primarily of four- and three-sided tasks. After the protocol was amended to require performance of a minimum number of two- and one-walled targets during each session, improved performance on these conditions was observed. However, the Yorkshire pigs had been terminated from testing by the time procedures were revised, and thus did not benefit from the revision. Moreover, this change in training made it extremely difficult for the micro pigs to achieve stringent criteria of Hopkins et al. (1996) for all facets of task acquisition.

Taken together, the failure of all subjects to meet the criteria for SIDE task acquisition may reflect the limitations first imposed by procedural methodology issues, and visual and motor skill limitations, rather than learning deficits. Although their performance was limited compared to primates tested, that they were able to perform as successfully as they did on one-walled targets suggests they acquired some important aspects of the task demands. However, it is impossible to determine to what extent their ability to demonstrate conceptual understanding of the SIDE task may have been constrained by their perceptual and motor capacities. Nonetheless, evaluation of their terminal test results showed that all pigs improved their performance with respect to the various target positions. This improvement was particularly noteworthy for the Yorkshire pigs (Hamlet and Omelet), who completed only a few 100 trials in their 10 weeks of training on the task. Furthermore, the high level of performance attained by one of the micro pigs (Ivory), regardless of target position or number of walls, strongly suggests some level of conceptual acquisition of the task.

In summary, the results of the present study underscore the importance of understanding the basic perceptual and motor capabilities of a species prior to developing appropriate methods of testing their cognitive abilities. While the joystick-operated video-game paradigm has proven suitable for testing several species, including monkeys, pigeons, and chimpanzees (Rumbaugh et al., 1989; Washburn et al., 1990; Spetch et al., 1992; Hopkins et al., 1996), it is not optimal for testing the cognitive abilities of pigs, as their performance was clearly hindered by dexterity limitations and visual constraints. Thorough investigations of the pig's visual and motor capabilities are necessary before their cognitive abilities can be adequately assessed using this or any type of technology. Use of a computer touch screen may better address the problem of limited dexterity and would likely provide a more viable alternative in future computer-interfaced studies of the cognitive abilities of pigs.

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 Pennsylvania State University, State College, Pennsylvania, United States.

AUTHOR CONTRIBUTIONS

All data collection was performed by CC. Data analyses were conducted by CC and SB. Contributions to the experimental design by SB. Writing and editing of the paper was conducted by CC and SB. Both authors contributed to the article and approved the submitted version.

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Do Emotional Cues Influence the Performance of Domestic Dogs in an Observational Learning Task?

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Using social information is not indiscriminate and being able to choose what to copy and from whom to copy is critical. Dogs are able to learn socially, to recognize, and respond to dog as well as human emotional expressions, and to make reputation-like inferences based on how people behave towards their owner. Yet, the mechanisms dogs use for obtaining and utilizing social information are still to be fully understood, especially concerning whether emotional cues influence dogs' social learning. Therefore, our main aim was to test the hypothesis that an emotionally charged (negative, positive, or neutral) interaction with the demonstrator of a "V" detour task prior to testing would affect subjects' performance, by: (i) changing the value of the information provided by the demonstrator or (ii) changing the valence of the learning environment. Our experimental design consisted of three phases: pre-test (subjects were allowed to solve the task alone); emotional display (dogs watched the unfamiliar human behaving in either a positive, negative or neutral way towards their owner); test (demonstrator showed the task and subjects were allowed to move freely). Only dogs that failed in pre-test were considered for analysis ($n = 46$). We analyzed four dependent variables: *success*, *time to solve the task*, *latency to reach the fence* and *matching* the side of demonstration. For each, we used four models (GEEs and GLMMs) to investigate the effect of (1) demographic factors; (2) experimental design factors (including emotional group); (3) behavior of the dog; and (4) side chosen and matching. All models took into account all trials (random effect included) and the first trials only. Our findings corroborate previous studies of social learning, but present no evidence to sustain our hypothesis. We discuss the possibility of our stimuli not being salient enough in a task that involves highly motivating food and relies on long and highly distracting interval between phases. Nevertheless, these results represent an important contribution to the study of dog behavior and social cognition and pave the way for further investigations.

Keywords: *Canis familiaris*, emotion, social cognition, social information, socially biased learning

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INTRODUCTION

Social life is advantageous in many ways. For instance, the possibility of an efficient communication between individuals (facilitated and maintained by signaling and perception) enables affiliative and/or cooperative interactions among social animals (Fedurek et al., 2015). Moreover, learning socially provides a flexible way of acquiring information that can reduce the costs often involved in the acquisition of resources and new skills (Zentall, 2006). Learning from others is key for the evolution of social behavior and allows children, as well as other animals, to acquire ecologically relevant information regarding their physical and social environment (Flynn and Whiten, 2013). Therefore, for individuals that live in cohesive groups, visual and acoustic cues, such as pointing, gazing, vocal and facial expressions act as important signals, thus, providing adaptive advantages for assessing and responding to experience without the need for direct interaction (Colbert-White et al., 2018).

Social learning can be defined as "learning facilitated by observation of, or interaction with, another individual or its products" (Heyes, 1994; Hoppitt and Laland, 2013). According to Canteloup et al. (2020), it can lead an organism to behave in a different way after watching another one act in a particular manner. Social learning usually occurs between conspecifics, that are well equipped with repertoires of social learning capacities to deal with the information provided by similar individuals (e.g., Whiten and Mesoudi, 2008; Legare, 2017). However, it often occurs between different species. This is the case for some bird species, as demonstrated by Seppanën and Forsman (2007), who has shown that migratory birds (flycatchers) can learn from resident birds (tits). The flycatchers used the other better-informed birds as a source of information and acquired their nest site preferences. Another example that has caught the attention of researchers involves dogs and humans. In fact, when looking at dogs, the investigation of interspecific processes is critical, due to their close and intimate relationship with people (e.g., Guillo and Claidière, 2020).

Social learning can ascribe a diversity of processes, such as social, local and stimulus enhancement, social facilitation, perceptual biases and others (Heyes and Galef, 1996; Hoppitt and Laland, 2013; Eschar et al., 2016; Lind et al., 2019). Taken together, these processes composite what authors such as Fragaszy and Visalberghi (2004) call socially biased learning. Goal-directed actions contain two main sources of information that can be gathered through observation: (i) the movement and (ii) the consequence. Imitation occurs when an observer learns specific aspects of another's actions, whilst emulation occurs when an observer learns about the effects of one's actions and copies the outcome (Heyes, 1993; Flynn and Whiten, 2013). However, the factors influencing whether what learning processes are in place for different animals in different contexts is an intriguing question (Fugazza et al., 2019). In several cases, a given behavior may have different weights depending on characteristics of the individual who is being observed (Canteloup et al., 2020). In fact, social learning strategies may differ greatly in form. Laland (2004), discusses the importance of assessing the nature of the strategies used during social learning, especially in term of the contexts where it occurs. According to Coelho et al. (2015), complementary to comprehending the underlying mechanisms is to address the questions "when to copy," "what to copy" and "whom to copy."

Such aspects are only actually beneficial if one is sensitive to and can remember how others have acted in past interactions. Humans, for example, since their first year of life tend to approach more individuals who have acted positively towards others and to avoid more individuals who have acted negatively, even though during development these preferences may not be as straight forward (Hamlin et al., 2011). In fact, the capacity to acquire new skills and knowledge by observing others is so critical to the development of humans that children as young as 2 years old will even imitate irrelevant actions (overimmitate) that they know are unnecessary to achieving an instrumental goal (Legare and Nielsen, 2015). However, the ability to imitate social partners is not restricted to humans. For instance, Caldwell and Whiten (2004) showed that common marmosets manipulate and interact more with an artificial fruit after a trained conspecific has given a full demonstration of how to open the artificial foraging task, compared to partial or no demonstration conditions, and Huber et al. (2020) have recently shown that dogs selectively imitate their caregivers, but not strangers.

The ability to discriminate individuals by their social role is critical for people. For instance, humans must assess the motivations, intentions and emotional reactions of others to make accurate decisions of who is and who is not an appropriate partner. In fact, this ability is found in human beings from very young ages, with preverbal infants already showing to evaluate others based on their behavior in different social contexts (Hamlin et al., 2007). The information individuals acquire is crucial to channel their decision-making (McFarland et al., 2013) and positive or negative third-party interactions might change the value of another individual as, for example, a social partner and, in a social learning context, someone that must be copied.

In addition to interacting with conspecifics, humans establish long lasting, dynamic, complex, and mutually advantageous relationships with domestic dogs (Albuquerque and Savalli, 2017; Savalli et al., 2019). They have co-existed for at least 10,000 years with genetic evidence suggesting more than 20,000 years of divergence between the ancestor of the modern gray wolf and the ancestor of the domestic dog (Skoglund et al., 2015; Pendleton et al., 2018). During this co-shared evolutionary history, dogs are believed to have developed cognitive capacities to better interact with humans (e.g., Nagasawa et al., 2015). For instance, they are very sensitive to human communicative cues (Hare et al., 2002; Reid, 2009; Dahas et al., 2013; Ford et al., 2019), in addition to producing signals to communicate with people (Savalli et al., 2014, 2016), and having the capacity to process, recognize and respond to human emotional expressions (Albuquerque et al., 2016, 2018; Somppi et al., 2016; Albuquerque, 2017; Kujala, 2018). Moreover, these animals can obtain information from humans about a novel object or an uncertain situation by observing their reactions towards the stimulus (Merola et al., 2012).

Dogs are sensitive to the behavior of others and use the social information they obtain from direct and indirect social interactions to solve problems (e.g., Topál et al., 2006; Range et al., 2007), both from conspecifics (Scandurra et al., 2016) and from humans (Pongrácz et al., 2001, 2003). In the early 2000's, Pongrácz and colleagues investigated whether dogs could learn socially. In 2001, they used a detour task, where dogs should reach a desired object positioned on one of the sides of a "V" shaped fence. Dogs showed a low rate of success when the movement was inwards. However, when a person was included as a demonstrator to show how to solve the problem, subjects decreased the time they took to solve the task and became proficient at the task in both directions.

On the other hand, dogs act differentially towards people even after a brief exposure to them. This happens because, like humans, domestic dogs can assign reputation-like statuses to other individuals that will be taken into account when choosing with whom to interact (Kundey et al., 2011). These assessments can occur directly but also indirectly, through the observation of third-party interactions. In fact, dogs can discriminate a generous from a selfish food-sharing person from observing the interaction between two people (e.g., Marshall-Pescini et al., 2011). Research has shown this discriminatory capacity may be more related to the presence of food than to the actual evaluation of the social role of each person (Piotti et al., 2017), however, Chijiiwa et al. (2015) controlled for these possible confounding effects and showed that dogs are indeed capable of assessing third-party interactions, discriminate social roles (e.g., helper vs non helper) and avoid the person who has behaved negatively towards their owner. Carballo et al. (2016, 2017) discuss that both the domestication process and the amount of experience dogs have with people influence these abilities.

Even though there is an increasing body of literature on dogs' abilities to learn from observation, to make reputation-like inferences and to recognize emotional expressions of humans, little is known about the influence affective cues and/or affective impressions pose on the capacity to obtain context-relevant information and to learn socially. In this study, we used the "V" detour task and a demonstrator with potentially different social weights, which were determined by her immediately prior interaction with the dog's owner in the presence of the dog. The demonstrator of the task, who was completely unfamiliar to the subject at that time, acted in either a positive, a negative or a neutral way towards the owner during a conversation. We combined adaptations of the classical "V" detour setting (Pongrácz et al., 2001, 2003) with a very thorough behavior codification of 46 analyzed subjects to better comprehend the nuances involved in domestic dogs' social learning, including what mechanisms are used in this sort of observational learning task. The experimental design consisted of three phases: pre-test (subjects were allowed to solve the task alone); emotional display (dogs watched the unfamiliar human behaving emotionally towards their owner); test (demonstrator showed the task and subjects were allowed to move freely).

We tested the hypothesis that the observation of third-party affective interactions between owner and demonstrator of the social learning test can either facilitate or impair subjects' learning (measured by completion of the task) depending on the valence of the interaction. We predicted the emotional displays by the unfamiliar person would affect the context in two ways: (i) changing the valence of the environment/situation (i.e., positive interaction would create a positive environment and could facilitate learning) and/or (ii) changing the value of the demonstration and, consequently, of the information regarding the detour (i.e., positive demonstrators would be seen by the dogs as providers of higher quality or more relevant information and negative demonstrators would be seen as having less relevant or lower quality information). Therefore, we expected dogs in the positive group to show higher rates of success, lower time to solve the task, higher matching (i.e., choosing the same side as demonstrator) and lower latencies, followed by dogs in the neutral group and, last, by dogs in the negative group. Moreover, we looked at other behaviors (looking at owner, standing still next to the owner, persistence, distraction, and time spent looking at demonstrator during demonstration of the task) in relation to the emotional group subjects had been assigned to in order to have a fuller understanding of the phenomena.

MATERIALS AND METHODS

Ethics Statement

All experimental procedures complied with the ethical guidance for the use of animals produced by the International Society for Applied Ethology. The study was approved by the Animal Ethics Committee of the University of São Paulo (USP) (CEUA n^o 1567110915) and did not involve any invasive measurements or caused any psychological discomfort to the subjects. The behavior of the dogs were monitored throughout the entire experimental session and in case of signs of distress, testing was terminated. Prior to the start of the experimental session, the owner was informed about the general lines of the study and signed a consent form.

Subjects

We tested a total of 52 healthy well socialized family adult dogs of various breeds. However, six dogs had to be excluded from the analyses due to having had success in the pre-test (see below for detailed information). Therefore, we analyzed the behavior of 46 dogs (30 females and 16 males), aged between 2 and 10 years old (**Table 1**). Participation was voluntary. The study was advertized in social media platforms, as well as in veterinary clinics, pet stores, etc., and owners voluntarily applied for participation. Suitable dogs, i.e., dogs that were used to be in unfamiliar places and to interact with unfamiliar people, were recruited after a screening process that consisted in a written semi-structured interview filled in by the owners prior to the experiment day.

Experimental Procedures

Data collection was conducted at the External Ethology Laboratory of the Institute of Psychology of USP, during a period of 12 months. The experimental environment consisted of two open-air spaces (**Figure 1**). In space A, the emotional demonstration phase was conducted, whereas pre-test and test were conducted in space B. Experimenter 1 (E1; demonstrator), who was always the same person between dogs, stayed hidden until the experiment started in order to guarantee the subject had absolutely no experience with her. Experimenter 2 (E2), who could vary between testing days, was trained to meet the owner and the dog outside the laboratory and provide the instructions of the experiment. Before the beginning of the experiment, dogs were given a period of free time (approxixmately 10 min) to explore the environment, so they would lose interest in the area, and get habituated and comfortable. From the

TABLE 1 | Information of the sample of dogs analyzed.

Dog	Emotional group	Side of 1st demonstration	Sex	Age (months)	Breed
1	Negative	Left	Male	48	Mongrel
2	Negative	Right	Female	48	Mongrel
3	Positive	Left	Male	48	Mongrel
4	Negative	Right	Male	30	Mongrel
5	Positive	Right	Female	96	Mongrel
6	Positive	Right	Female	84	Border Collie
7	Negative	Left	Female	15	Mongrel
8	Negative	Right	Female	84	Lhasa Apso
9	Positive	Left	Female	60	Havanese
10	Negative	Right	Male	69	Shetland Sheepdog
11	Positive	Left	Male	24	Shetland Sheepdog
12	Positive	Right	Female	48	Mongrel
13	Negative	Left	Female	72	Golden Retriever
14	Negative	Left	Male	72	Mongrel
15	Positive	Right	Female	72	Rottweiler
16	Negative	Left	Male	60	Mongrel
17	Positive	Right	Female	96	Mongrel
18	Negative	Left	Female	60	Mongrel
19	Positive	Right	Female	60	Pitbull
20	Negative	Left	Male	36	West Terrier
21	Positive	Left	Male	15	French Bulldog
22	Neutral	Left	Male	36	Mongrel
23	Negative	Left	Female	36	Mongrel
24	Neutral	Left	Male	24	Poodle
25	Neutral	Right	Male	48	Yorkshire
26	Neutral	Left	Female	102	Mongrel
27	Neutral	Left	Female	30	Pug
28	Neutral	Left	Female	24	Mongrel
29	Positive	Right	Female	60	Australian Cattle Dog
30	Neutral	Right	Female	96	Daschund
31	Positive	Right	Female	60	Rottweiler
32	Neutral	Right	Female	57	Labrador
33	Neutral	Left	Male	96	Labrador
34	Neutral	Left	Female	36	Labrador
35	Neutral	Right	Female	20	Mongrel
36	Negative	Right	Female	60	Schnauzer
37	Neutral	Left	Female	16	Pitbull
38	Negative	Left	Female	36	French Bulldog
39	Neutral	Right	Female	48	English Cocker Spaniel
40	Negative	Right	Male	123	Sheepdog
41	Neutral	Left	Male	21	Mongrel
42	Neutral	Right	Male	42	Mongrel
43	Positive	Left	Female	96	Yorkshire
44	Neutral	Right	Female	19	Pinscher
45	Negative	Right	Female	84	Mongrel
46	Neutral	Right	Female	114	Poodle

moment E2 and owner understood the dog was habituated, the experiment was started.

Subjects were tested in an adapted form of the classic "V" detour task (Pongrácz et al., 2001, 2003), where dogs are placed in front of a V-shaped fence with a baited bowl in its inner vertex (**Figure 2**) and witness a demonstration from a knowledged individual (human) of how to access the bowl. The experiment was divided into three distinct experimental phases: pre-test (subjects allowed to solve the task alone); emotional display (dogs watched the unfamiliar experimenter behaving in either a positive, negative or neutral way towards the owner); test (experimenter demonstrated the task and subjects were allowed to solve it). Each dog was tested in 10 similar trials that only differed on side of demonstration (left or right), which was counterbalanced along trials. First side of demonstration was randomized between subjects. Only dogs that were not successful in pre-test were considered for analysis (n = 46). E1 acted as the person who interacted emotionally (positive manner, negative manner, or neutral manner) towards the owner and as the demonstrator of the social learning task. E1 only interacted with the dog after the experiment was finalized.

All experimenters were trained before the start of the experiment. The emotional displays (see below) were extensively trained with E1 until the sentence pronunciation and emotional cues were consistent and robust.

Pre-test

Immediately after habituation, E2 instructed the owner about pre-test, which would be a trial without the demonstrator to see whether the dog could solve the detour task alone: if they could, that would mean that no social learning would occur. Therefore, performance on the pre-test served as a criterion to include – or not – the dogs in the analysis.

As soon as E2, owner and dog entered space B (see **Figure 1**), E2 took them to the previously marked area (3.5 m away from the vertex of the fence) where owner and dog would stand during the demonstration of the task in the test phase, and instructed the owner to walk towards the outer vertex of the fence in a straight line in order to let the dog see the baited bowl. The dog was on the leash at this point. The bowl, which was on the inner vertex of the fence, was not reachable, but was visible and the dogs could smell the food inside. As soon as the dog appeared interested to get the food, E2 instructed the owner to come back to the marked area. Once owner and dog were set, E2 gave the command and the owner unclipped the dog's leash. At this point, the dog could move completely free and the owner stood still, neutral and did not interact with the dog by any means. Whether the dog could reach the baited bowl in the inner vertex of the fence or not was recorded and used to select the subjects that would be considered in the data analysis. Each subject was allowed one pre-test that lasted 15 s. After this time, the owner was asked to retrieve the dog and accompany E2 outside the experimental area.

Emotional Display Phase

In the meanwhile, E1 entered the experimental area and stayed between space A and B. This particular area had an opaque door separating space A, which E1 closed after her entrance. That way, dog and owner could return to space A without seeing E1. The owner was instructed to stay still, looking at the demonstrator and to keep a neutral facial expression and body position. In addition, they should never interact with the dog, who was on the leash but

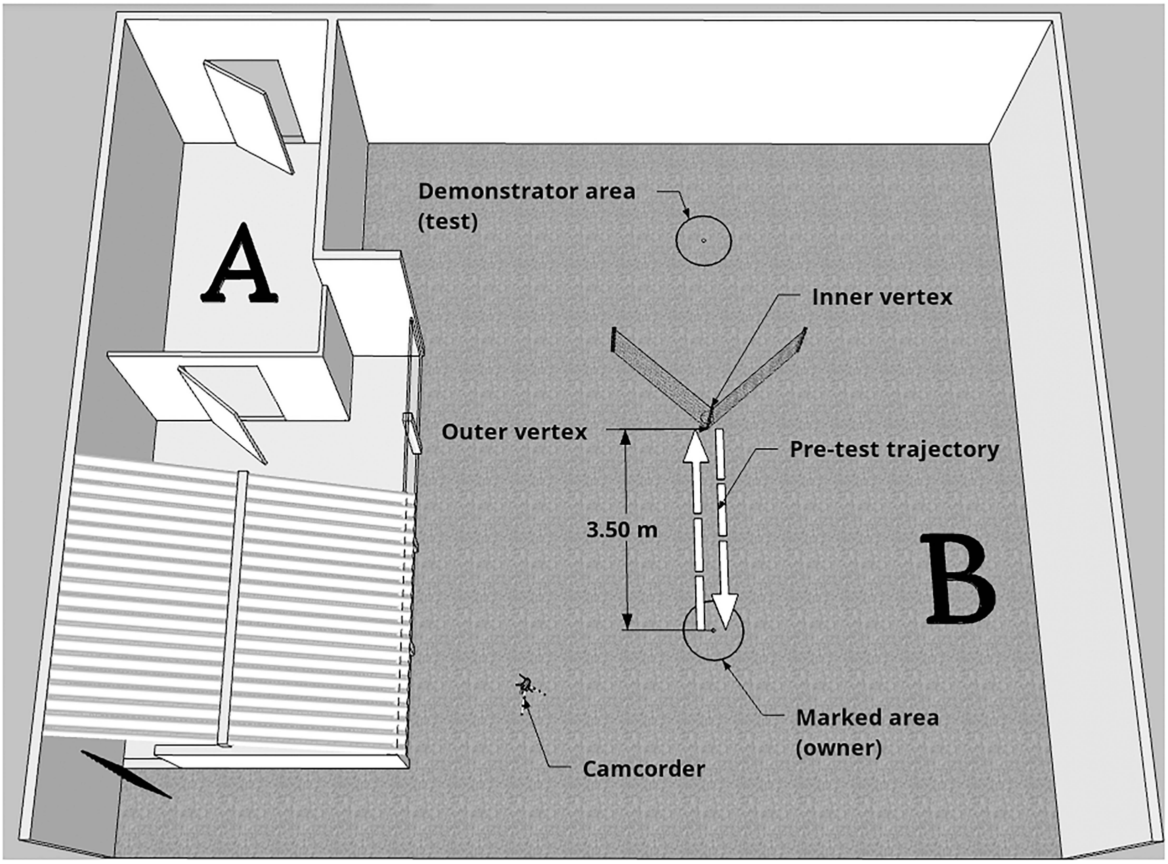

FIGURE 1 | Schematic representation of the experimental area. The emotional display phase happened in Space A, whereas pre-test and test occurred in Space B. Dashed arrows represent the trajectory taken by the owner and dog during pre-test (with the aim of showing the dog the baited bowl placed in the inner vertex of the fence).

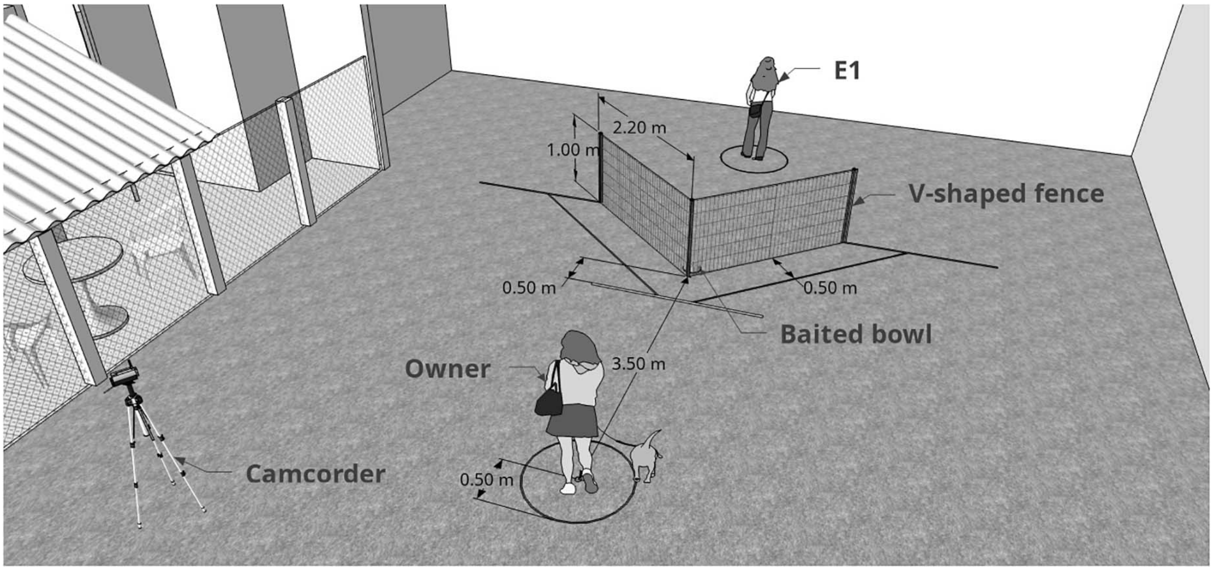

FIGURE 2 | Graphic representation of the moment when the subject was about to be released and start the test. E1 (demonstrator) had already baited the bowl and was distant from the fence, facing the opposite side). The difference between pre-test and test is the presence of the demonstrator. Measurements shown are those from the real experiment.

FIGURE 3 | Example of the emotional display phase. **(A)** Shows where the owner was positioned, **(B)** depicts a positive emotional display, and **(C)** depicts a negative emotional display.

could move. As soon as the owner and dog were positioned in the pre-determined area (see **Figure 3** for an example), E1 entered space A making eye-contact solely with the owner. The display of the emotional stimulus occurred only once for each subject and was directed to the person. The stimulus could be either positive, negative or neutral and consisted of the pronunciation of the sentence "You know what I mean," in English, in order to avoid any familiarity or habituation effect with any of the words used by the Brazilian owners with their dogs. The sentence was repeated three times, each with the intonation correspondent to the designated valence, together with the congruent body and facial emotional cues (**Figure 3**). Dogs were previously allocated to one of the three groups: positive, neutral or negative in a randomorder.

Test

After the emotional interaction, E1 left space A through the opaque door (still in the character, i.e., positive, neutral or negative) and E2 entered space A to continue guiding the owner. While E2 was providing the instructions regarding the next phase of the test, E1 positioned herself at the outer vertex of the fence, standing still, with a neutral face and treat bag clipped to her belt. Once set, owner, dog and E2 entered space B and positioned themselves in the pre-determined area (the same as in pre-test). At this stage, the owner stood still with a neutral face and body position throughout the entire test, never interacted with the dog regardless of their behavior and looked straight ahead. Subjects who had their owner interfering in any way were excluded from analyses. Soon after everyone was set in place, E1 clapped her hands three times to gain the subject's attention to start the silent demonstration of the detour task. Once eye contact was established, she initiated the detour using one side of the fence (previously determined and randomized between subjects). When she reached the bowl, she leaned down, put treats (small pieces of fresh cheese and sausage) from her bag inside and then moved away from the set up to the previously determined area (demonstrator area, see **Figure 1**). From this point until the end of the trial, she kept her back turned to the setting, keeping a neutral manner, and did not move or looked at the dog (see **Figure 2**). E2 gave the owner the command to unclip the leash. The dog was then free to move freely for 30 s. Success was considered when the subject reached the bowl within this period. If the dog completed the task before 30 s, E2 asked the owner to bring back the dog after letting them eat the food. Dog's behavior was recorded by a digital video camera for *post hoc* analysis. After this period, E2 asked the owner to retrieve the dog and come back to the marked position. Each dog was presented to 10 trials, alternating side of demonstration, which consisted of repetitions of the above mentioned. Before pre-test and test, to avoid potential olfactory cues, the demonstrator walked around the fence ten times (five deviations to the left side and five deviations to the right side).

Data Coding and Statistical Analysis

During testing, E2 manipulated a chronometer, used to control for testing time, and a paper sheet, where she/he marked whether the dog had success, the time to solution and the chosen side in each trial. However, in order to generate more robust data and collect more detailed information, we analyzed the videos with the software Solomon Coder Beta[1] using real speed and frame-by-frame coding, looking at the mentioned variables and also another complementary behaviors.

A second naïve person coded a random sample of 25% of the videos. Both coders were blind to the test group of all dogs and Kendall's concordance coefficient was calculated: time watching the demonstrator during test ($W = 0.97$), looking at the owner ($W = 0.74$), looking at the bowl ($W = 0.83$), latency to reach the fence ($W = 0.93$), sniff the fence ($W = 0.67$), and, sniff the environment $W = 0.76$).

We analyzed four main dependent variables: *success* in solving the task, *time to solve the task* for those who solved it, *latency to reach the fence* (defined as the time the subject took to arrive at the outer vertex of the fence) and *matching* of side, i.e., when the dog chose the same side as the demonstration. Matching and latency to reach the fence were also used as independent variables for verifying potential effects on the other response variables. Success in solving the task and matching, which were binary responses, were analyzed using a binomial generalized linear mixed model (GLMMs) with a logit link function and dog as a random effect when considering all trials. A logistic regression was used when considering the first trial only. For these models, estimates were presented as odds ratio (OR). Time to solve the task and latency

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[1] www.solomoncoder.com

to reach the fence were analyzed using a linear mixed model (LMMs) with dog as a random effect when considering all trials. Regression models were run when considering the first trial only.

For each dependent variable, we used four models: (1) effect of demographic factors (sex, age and breed); (2) effect of experimental design factors (emotional stimulus, trial segment and side of demonstration); (3) effect of behavior of the dog (time spent watching the demonstrator during the test, whether the dog looked at the owner for some time (yes/no), whether the dog stood still next to the owner for some time (yes/no), persistence score (defined below), distraction score (defined below), duration until reaching the fence (latency to reach the fence) – except when this variable was the response; and (4) effect of side chosen by the dog and matching – except when this variable was the response. A "side chosen" was considered as soon as the dog had passed the outer vertex of the fence in one of the two possible directions: left or right. This measure has been chosen to verify any side biases and to test for how dogs match their behavior to that of the demonstrator. All models were conducted using all trials (random effect included) and the first trials only. For models with all trials, segments of trials were used as factor to evaluate the learning effect. To do so, trials were divided into three categories (initial: the first three trials, middle: the four middle trials, and, final: the final three trials). For analysing the behavior of dogs, we used what we called "persistence score" and "distraction score." Persistence score was defined as the number of behaviors presented among the list of actions: digging in front of the fence, touching the fence, sniffing the fence, and looking at the bowl. Distraction score was defined as the number of behaviors presented among the list of actions: urinating, defecating, seeking for noises, sniffing the environment, and digging the ground. We chose to divide the analysis in different models because we considered that each group of variables intended to evaluate a different facet of the phenomenon studied.

Prior to running the models, in order to evaluate the homogeneity of groups of dogs distributed among emotional stimulus (positive, negative or neutral) with respect to sex, breed and the side of first demonstration, we used the Chi-square test. In addition, with respect to the dogs' age, we used the one-way Analysis of Variance.

All behaviors were coded from the records of the test phase, mostly from when the dog was free to move in the setting. In addition, we analyzed the behavior "time spent looking at demonstrator" during the demonstration of the task by E1, which was not accounted for when dogs had been unclipped, because at that point, E1 was away from the fence, facing backwards and standing completely still and dogs showed very little or no interest in her. Data was collected for the entire test, however the dogs almost never looked at the demonstrator when they were free to move, meaning that we had too many zeros and, thus, could only analyse data from when the dogs were still on the leash. On the other hand, the other behaviors have not been accounted for during demonstration, because at that point, dogs were on the leash, next to the owner, and mostly visually following the demonstrator.

Models residuals and fitting were checked. The software SAS University Edition was used for all statistical analyses. We used a 5% significance threshold with Bonferroni correction for each model for interpretation of the results. The significance level for models 1–4, were, respectively, 1.7, 1.7, 0.8, and 2.5%. The ethogram used for behavioral codification is included in supplementary materials as **Supplementary Table 1**.

RESULTS

From a total sample of 52 tested dogs, the six dogs who passed pre-test had to be excluded from analysis. Thus, the sample analyzed consisted of 46 subjects (30 females and 16 males) with an average age of 52.1 months (standard deviation = 28.8), of various breeds (27 purebred and 19 mongrels). From the sample, 33 solved the task in the first test trial. Trials altogether were a total of 460 (two missing trials), from which 150 ended up in success. Regarding the emotional display groups, 16 dogs were exposed to the negative emotional stimulus, 16 to the neutral stimulus and 13 to the positive stimulus.

Since a few dogs were excluded, we analyzed whether the distribution among emotional groups (positive, negative, and neutral) was balanced for demographic variables and side of first demonstration. We found no bias for sex (male vs female), breed (purebred vs mongrel), age and side (left or right).

In model 1, in which we took into account the demographic characteristics of the subjects (i.e., sex, age, and breed), we found only an effect of age on matching, when looking at all trials ($F_{1,179}$ = 7.53, p = 0.0067). The greater the age the smaller the odds of matching (Odds Ratio = 0.965, CI95% = [0.941;0.990]). No effect was found for success, time to solve the task and latency to reach the fence (**Table 2**).

Regarding the second model, in which we included the experimental design aspects (i.e., emotional stimulus received in the emotional display phase, trial segment, and side of demonstration), we only found a significant effect for trial segment. In the final segment of trials the odds of success were greater when compared to the initial segment ($F_{1,410}$ = 5.33, p = 0.0215; OR = 1.999, CI95% = [1.108;3.605]), and to the middle segment ($F_{1,410}$ = 12.31, p = 0.0005; OR = 2.7234, CI95% = [1.554;4.774]). Moreover, time to solve the task (measured in seconds), when there was success, decreased across segment of trials ($F_{2,121}$ = 8.36, p = 0.0004); initial estimate: 19.679, CI95% = [17.368;21.989]; middle estimate: 18.021, CI95% = [15.775;20.267]; final estimate: 14.964, CI95% = [12.733;17.196]). Initial and final segment were significantly different regarding the time to solve the task ($F_{1,121}$ = 15.88, p = 0.0001), as well as the middle and final segment ($F_{1,121}$ = 7.43, p = 0.0074). On the other hand, latency to reach the fence was significantly lower in the initial trials when compared to the middle and final trials ($F_{2,410}$ = 6.72, p = 0.0013, initial estimate: 11.915, CI95% = [8.918;14.912]; middle estimate: 14.022, CI95% = [11.115;16.929]; final estimate: 15.773, CI95% = [12.770;18.775]). Initial and middle segments were significantly different regarding latency to reach the fence ($F_{1,410}$ = 4.60, p = 0.0325), as well as the initial and final segment of trials ($F_{1,410}$ = 3.15, p = 0.0003). No aspect of the experimental design influenced the odds of matching (**Table 2**). Valence of

TABLE 2 | Summary of the results of the models (statistic and *p*-value).

	Response variables							
	Success in solving the task		**Time to solve the task**		**Latency to the fence**		**Matching**	
Models	**All trials**	**1st trial**	**All trials**	**1st trial**	**All trials**	**1st trial**	**All trials**	**1st trial**
Model 1 – Effect of demographic factors								
Sex	$F_{(1,412)} = 0.24$ $p = 0.6210$	$X_1^2 = 0.30$ $p = 0.5829$	$F_{(1,123)} = 1.63$ $p = 0.2041$	$F_{(1,9)} = 0.34$ $p = 0.5755$	$F_{(1,412)} = 1.77$ $p = 0.1847$	$F_{(1,42)} = 0.01$ $p = 0.9066$	$F_{(1,179)} = 0.63$ $p = 0.4276$	$X_1^2 = 0.51$ $p = 0.4749$
Age	$F_{(1,412)} = 1.67$ $p = 0.5703$	$X_1^2 = 1.74$ $p = 0.1873$	$F_{(1,123)} = 0.03$ $p = 0.8658$	$F_{(1,9)} = 0.73$ $p = 0.4137$	$F_{(1,412)} = 0.31$ $p = 0.5750$	$F_{(1,42)} = 0.62$ $p = 0.4348$	$F_{(1,179)} = 7.53$ **$p = 0.0067$**	$X_1^2 = 3.87$ $p = 0.0493$
Breed	$F_{(1,412)} = 0.32$ $p = 0.5702$	$X_1^2 = 0.11$ $p = 0.7418$	$F_{(1,123)} = 0.18$ $p = 0.6753$	$F_{(1,9)} = 0.04$ $p = 0.8444$	$F_{(1,412)} = 0.20$ $p = 0.6541$	$F_{(1,42)} = 0.21$ $p = 0.6465$	$F_{(1,179)} = 1.78$ $p = 0.1843$	$X_1^2 = 0.46$ $p = 0.4964$
Model 2 – Effect of experimental design								
Emotional stimulus	$F_{(2,410)} = 0.40$ $p = 0.6675$	$X_1^2 = 0.64$ $p = 0.7275$	$F_{(2,121)} = 1.50$ $p = 0.2277$	$F_{(2,9)} = 0.88$ $p = 0.4474$	$F_{(1,410)} = 0.25$ $p = 0.7796$	$F_{(2,42)} = 1.71$ $p = 0.1933$	$F_{(2,177)} = 1.41$ $p = 0.2466$	$X_2^2 = 0.21$ $p = 0.9016$
Trial segment	$F_{(2,410)} = 6.28$ **$p = 0.0021$**	–	$F_{(2,121)} = 8.36$ **$p = 0.0004$**	–	$F_{(1,410)} = 6.72$ **$p = 0.0013$**	–	$F_{(2,177)} = 1.39$ $p = 0.2525$	–
Side of demostrantion	$F_{(1,410)} = 0.06$ $p = 0.8072$	$X_1^2 = 0.08$ $p = 0.7799$	$F_{(1,121)} = 0.52$ $p = 0.4714$	$F_{(1,9)} = 2.94$ $p = 0.1208$	$F_{(1,410)} = 2.74$ $p = 0.0989$	$F_{(1,42)} = 1.55$ $p = 0.2193$	$F_{(1,177)} = 0.87$ $p = 0.3525$	$X_1^2 = 0.36$ $p = 0.5497$
Model 3 – Effect of behaviour of the dog								
Time watching demonstrator (test)	$F_{(1,406)} = 0.08$ $p = 0.7763$	$X_1^2 = 0.39$ $p = 0.5306$	$F_{(1,117)} = 0.33$ $p = 0.5671$	$F_{(1,6)} = 0.17$ $p = 0.6944$	$F_{(1,407)} = 15.37$ **$p = 0.0001$**	$F_{(1,40)} = 11.89$ **$p = 0.0013$**	$F_{(1,173)} = 0.29$ $p = 0.5900$	$X_1^2 = 2.43$ $p = 0.1186$
Whether the dog looked at the owner	$F_{(1,406)} = 22.68$ **$p < 0.0001$**	$X_1^2 = 2.49$ $p = 0.1148$	$F_{(1,117)} = 0.70$ $p = 0.4051$	$F_{(1,6)} = 0.14$ $p = 0.7250$	$F_{(1,407)} = 0.08$ $p = 0.7712$	$F_{(1,40)} = 0.85$ $p = 0.3625$	$F_{(1,173)} = 0.60$ $p = 0.4387$	$X_1^2 = 0.002$ $p = 0.9640$
Whether the dog stood still next to the owner	$F_{(1,406)} = 0.61$ $p = 0.4352$	$X_1^2 = 0.09$ $p = 0.7674$	$F_{(1,117)} = 1.76$ $p = 0.1868$	$F_{(1,6)} = 0.38$ $p = 0.5598$	$F_{(1,407)} = 89.13$ **$p < 0.0001$**	$F_{(1,40)} = 16.48$ **$p = 0.0002$**	$F_{(1,173)} = 1.24$ $p = 0.2674$	$X_1^2 = 0.57$ $p = 0.4510$
Persistence score	$F_{(1,406)} = 2.72$ $p = 0.0997$	$X_1^2 = 1.00$ $p = 0.3159$	$F_{(1,117)} = 42.52$ **$p < 0.0001$**	$F_{(1,6)} = 5.10$ $p = 0.0646$	$F_{(1,407)} = 258.75$ **$p < 0.0001$**	$F_{(1,40)} = 19.01$ **$p < 0.0001$**	$F_{(1,173)} = 0.00$ $p = 0.9460$	$X_1^2 = 0.11$ $p = 0.7370$
Distraction score	$F_{(1,406)} = 2,51$ $p = 0.1141$	$X_1^2 = 0.17$ $p = 0.6771$	$F_{(1,117)} = 11.98$ **$p = 0.0007$**	$F_{(1,6)} = 0.06$ $p = 0.8201$	$F_{(1,407)} = 9.00$ **$p = 0.0029$**	$F_{(1,40)} = 0.14$ $p = 0.7132$	$F_{(1,173)} = 0.90$ $p = 0.3445$	$X_1^2 = 0.67$ $p = 0.4116$
Latency to reach the fence	$F_{(1,406)} = 31.66$ **$p < 0.0001$**	$X_1^2 = 2.66$ $p = 0.1028$	$F_{(1,117)} = 59.23$ **$p < 0.0001$**	$F_{(1,6)} = 7.90$ $p = 0.0307$	–	–	$F_{(1,173)} = 0.50$ $p = 0.4802$	$X_1^2 = 1.72$ $p = 0.1892$
Model 4 – Effect of choice								
Side chosen by the dog	$F_{(1,177)} = 3.94$ $p = 0.0488$	$X_1^2 = 0.30$ $p = 0.5817$	$F_{(1,121)} = 0.88$ $p = 0.3510$	$F_{(1,10)} = 0.27$ $p = 0.6154$	$F_{(1,177)} = 0.63$ $p = 0.4279$	$F_{(1,20)} = 2.46$ $p = 0.1323$	$F_{(1,178)} = 2.23$ $p = 0.1373$	$X_1^2 = 0.006$ $p = 0.9402$
Matching	$F_{(1,177)} = 0.66$ $p = 0.4187$	$X_1^2 = 0.005$ $p = 0.9468$	$F_{(1,121)} = 0.92$ $p = 0.3403$	$F_{(1,10)} = 0.39$ $p = 0.5481$	$F_{(1,177)} = 1.39$ $p = 0.2394$	$F_{(1,20)} = 0.62$ $p = 0.44090$	–	–

For each dependent variable (success, time to solve the task, latency to reach the fence and matching) there are models for all trials and for the first trial. Due to correction for multiple comparisons (Bonferroni approach) the significance level adopted for the models 1–4, were, respectively, 1.7, 1.7, 0.8, and 2.5%).

the emotional display phase (neutral, positive, or negative) and side of demonstration had no effect on the dependent variables considered (**Figure 4**).

For the third model, we investigated the effect of the behavior of the dog measured by (i) time watching the demonstrator during demonstration of the task, (ii) whether dogs looked at the owner, (iii) whether dogs stood still besides the owner, (iv) persistence score (e.g. not making the detour), (v) distraction score, and (vi) latency to reach the fence. Considering all trials, the odds of success in the task were significantly smaller when the dog looked at the owner at some point ($F_{1,406} = 22.68$, $p < 0.0001$, OR = 0.031, CI95% = [0.008;0.131]). Moreover the greater the latency to reach the fence the smaller the odds to succeed ($F_{1,406} = 31.66$, $p < 0.0001$, OR = 0.874, CI95% = [0.833;0.916]). All other behaviors did not influence the odds of success in the task. When considering only the first trial, no effect on success was found (**Table 2**). For time to solve the task, we found an effect of persistence ($F_{1,117} = 42.52$ $p < 0.0001$), distraction ($F_{1,117} = 11.98$ $p = 0.0007$) and latency to reach the fence ($F_{1,117} = 59.23$ $p < 0.0001$): time to solve the task increased when these behaviors increased (see **Figure 4**). When considering only the first trial, for latency to reach the fence, we found an effect of time watching the demonstrator during demonstration of the test ($F_{1,407} = 15.37$ $p = 0.0001$), persistence score ($F_{1,407} = 258.75$ $p < 0.0001$) and distraction score ($F_{1,407} = 9.00$ $p = 0.0029$), all factors were inversely related to latency to reach the fence. Contrarily, latency to reach the fence was greater for dogs that stood still next to the owner (estimate = 19.36, CI95% = [17.79; 20.92]) than for those that did not (estimate = 11.11, CI95% = [9.78;12.44]). These results were also observed when considering only first trials, except for distraction (**Table 2**).

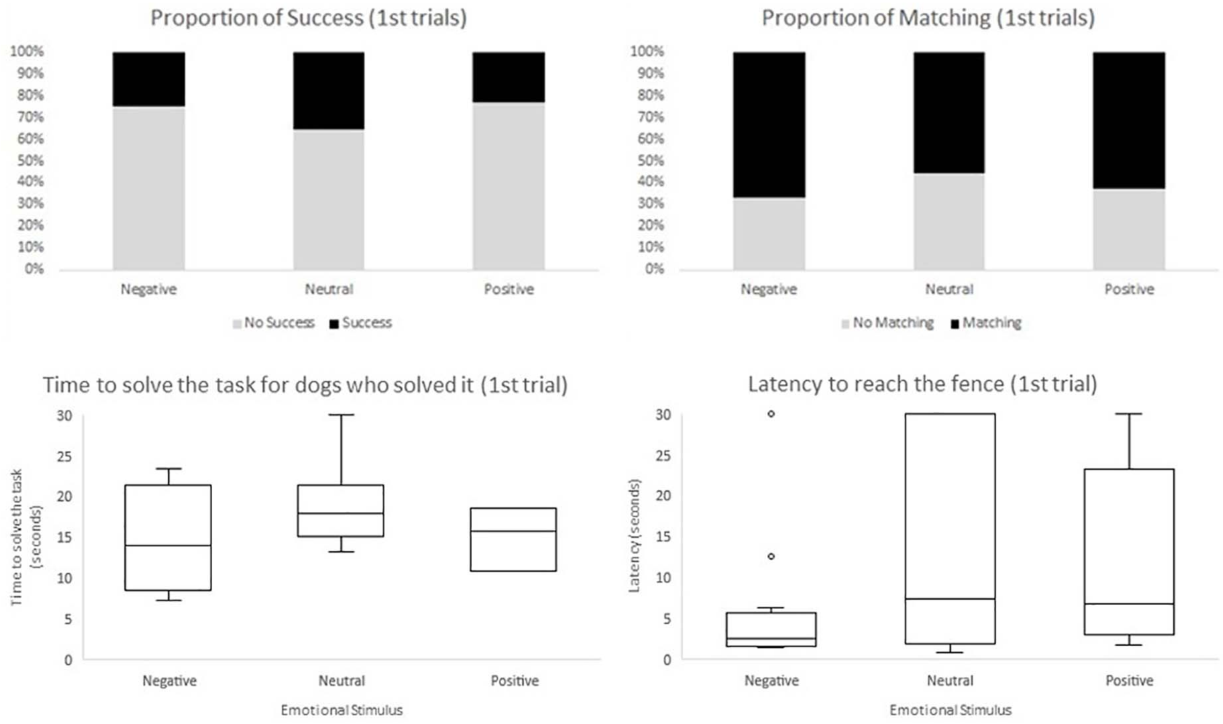

FIGURE 4 | Descriptives of the four dependent variables accounting the first trials, within each emotional group (negative, neutral, and positive). Shown as the proportion of success, the proportion of matching the side of demonstration and the box and whisker plot of time to solve the task and latency to reach the fence.

Finally, no significant effect of dogs' behaviors was found for matching (**Table 2**).

Lastly, model 4 investigated whether the side dogs chose and matching were related to having success in the task, time to solve the task and latency to reach the fence. Considering all trials, we found no effect regardless the variable.

DISCUSSION

Our results corroborate Pongrácz et al. (2001, 2003) findings regarding dogs' capacity to solve the detour task after witnessing the demonstration of the test by a knowledged individual. Pongrácz et al. (2001) observed that dogs alone could not solve a V-shaped detour task from the outside inwards. Therefore, they used a person to demonstrate how to solve the problem and showed that dogs learned from observing the demonstrator how to make the detour. In 2003, the research group used a similar task with a fence that had two open doors, one on each side, which allowed dogs to move through the fence in a faster and easier path to access the food. Pongracz and colleagues found that dogs could imitate humans and would prioritize the demonstrator's cues instead of their own experience. Even though they could use the doors, dogs made the detour after watching the demonstration. Dogs that did not see a demonstrator used the doors.

In our study, dogs' success increased as trial segment increased and the time dogs took to solve the task decreased along attempts, which indicates a learning effect across trial segments. Furthermore, when looking at latency to reach the fence, we found that subjects took less time to reach the fence in the initial trials. This last result can be explained by either (i) greater motivation in the beginning; (ii) loss of interest in the task with time and repetition; or (iii) tiredness. A possible explanation could be that dogs needed less time to move as they became proficient in solving the task. However, we found that success was lower when latency to reach the fence was higher, meaning that this latter explanation is unlikely true and some other mechanisms must be in place.

Our results showed that age was the only factor to influence the variable matching (i.e., dogs choosing the same side as the demonstrator). For the analysis of all trials, the only significant effect found was that older dogs were less likely to match their choice with the behavior of the human demonstrator. Even when running a model with the variables "side chosen by dog" and "matching" as independent variables to investigate their potential effect on subjects' success, time to solve the task, and latency to reach the fence, no significant results were found for matching.

Our findings show that dogs were learning along the trials and were performing better and faster in the test with experience. They also show that dogs were not able to solve the task before the inclusion of a human demonstrator, corroborating previous studies and validating the task used in terms of social learning. However, dogs did not match the behavior of the demonstrator (see Fugazza et al., 2019 for a discussion on this topic). These results raise important questions regarding what sort of mechanisms dogs are using in the test. From our data, dogs are not copying or imitating the human demonstrator. We suggest other socially biased learning mechanisms are being used, such as local enhancement, stimulus enhancement and/or social facilitation (Heyes and Galef, 1996). Social facilitation occurs when the presence of a demonstrator increases the chances of the observer to perform the same action, whilst stimulus/local enhancement (Spence, 1937; Thorpe, 1956) happens when there is an interaction between a demonstrator and an object or a place increasing the chances of the observer to interact with the same object or move towards the same place. These are two of the most common processes that ground socially biased learning (Hoppitt and Laland, 2013). Taken from the characteristics of our setting and our task, not finding significant results for matching, means that local and stimulus enhancement are possible. Even though we tend to consider the demonstrator or the movement the demonstrator does the most salient stimuli, it is possible that, for dogs, the baited bowl is in fact more salient. If that is the case, the individual might use their time during testing to try passing the fence to reach the food, without processing the detour itself. Thus, the dog could keep trying to transpass in any direction, eventually succeeding to get to the end of the fence and to the food. Therefore, we must consider that the local in which the demonstrator arrives (baited bowl) and the stimulus in the inner vertex of the fence (baited bowl) might be functioning as the driver for the dogs' behavior. According to Heyes (1993) and other researchers such as Flynn and Whiten (2013), animals can learn the affordances of situations/contexts, in our case the V detour task, and emulate the outcome of another individual's behavior. If dogs are using emulation in this test, they would achieve the consequence of the task, i.e., getting to the baited bowl, without reproducing the same behavior or behavioral sequence of the demonstrator. In fact, Mersmann et al. (2011) have tested the hypothesis that dogs use simpler mechanisms than imitation to solve social learning tasks. Part of their study was to investigate the underlying mechanisms of dogs' performance in the V detour task and they argue that stimulus enhancement and affordance learning are powerful ways to solve this sort of problem for these animals. An interesting approach for further studies would be to look only at the subjects who completed the test within the same time as provided by pre-test, to deeper investigate the role of individual learning. Here, we have made a methodological choice to use a shorter duration at pre-test to control for habituation to the task while still providing enough time to solve the detour.

The analyses of the behavior of the dogs showed that success was lower if the dog looked at their owner at some point, when considering all trials, but not when analyzing first trials only. Possibly, in the cases when dogs looked at the owner, they did not know what to do and were trying to extract some information from their owner's potential reaction (e.g., Merola et al., 2014). Moreover, when considering all trials, we found that the greater the persistence score, the distraction score and latency to reach the fence, the higher the time to solve the task, which is explained by logical time allocation by the subjects. On the other hand, the greater the persistence score, the distraction score, and time spent looking at the demonstrator during the demonstration of the test, the lower the latency to reach the fence. This was true for both all trials and first trials only with the exception of the distraction score that had an effect only when analyzing all trials, which, again, could be explained by greater interest in the baited bowl in the beginning of the test. However, latency to reach the fence was higher when the dog stayed besides their owner, a result of logical time allocation.

Interestingly, the emotional group (positive, negative, or neutral) had no effect on any of the four dependent variables (success, time to solve the task, latency to reach the fence and matching).

Dogs are known to be very good readers of human gestures, such as pointing and gazing (Cabral and Savalli, 2020), human body postures (Vas et al., 2005), and human facial expressions (Albuquerque et al., 2016, 2018; Correia-Caeiro et al., 2020). Furthermore, studies such as those from Turcsán et al. (2015) and Buttelmann and Tomasello (2013) show that the perception of human emotional expressions can differentially guide dogs' behavior into choosing one of two objects and those of Merola et al. (2012, 2014) demonstrate that dogs obtain information from humans' emotional reactions in order to interact – or not – with an unfamiliar object or situation. Not only emotional expressions but the attitude of a person towards the owner can channel how dogs behave and change their response depending on what they have observed (Chijiiwa et al., 2015). Moreover, there is evidence (Müller et al., 2015) that dogs trained with negative emotional expressions learned the contingencies of their task slower than dogs trained with positive emotional expressions. However, in our study, the valence (positive, negative or neutral) of the emotional display phase did not affect subjects' performance.

Taking all the above into account, it is quite surprising that the emotional display our subjects witnessed in this study had no significant effect on their responses in this social learning task. One possible explanation is that the interval between the emotional display phase and the actual testing was too long and dogs did not remember what they have witnessed between the demonstrator and the owner. Fiset et al. (2003) studied dogs' operational memory and described an above chance performance in an object permanence task for up to 240 s without distractors. In our case, the temporal space between the emotional display phase and the test not only included several distractions (due to a very rich environment) but also was over the mentioned interval, taking at least 5 min for the transference from one phase to the other. In fact, taking memory into account is not only important as is necessary, especially when studying social animals, who live in cohesive groups. We believe that further exploring this issue is critical to understanding the influence of emotional cues on the performance of dogs in social learning tasks. We know that dogs are capable of discriminating and recognizing human emotional expressions (e.g., Albuquerque et al., 2016). However, there is still a lack of evidence regarding for how long these animals can store this sort of information in their memory. In 2018, Proops and colleagues showed that horses can remember human facial expressions in such way that after seeing pictures of a face showing positive or negative emotion, they will respond differently when later they are presented to the real person. This study shows that non-human animals can indeed remember facial expressions of humans, or at least the sensation of seeing them angry or happy. However, they presented the emotional stimuli to the horses for a longer time compared to our study, which may have been critical for the storage of the emotional information, and they did not use food in their experimental design, which can function as an important distraction from the task.

Another possible explanation is that the used emotional displays were not salient enough to change the value of the demonstrator or to change the valence of the experimental setting itself, especially because there was food involved (see Chijiiwa et al., 2015 for a discussion on that). As discussed above, the baited bowl may have worked as the salient stimulus for the dogs, instead of the emotionally charged demonstrator and the demonstrator's behavior during the task. At the same time, it is possible that the social learning task was too easy, thus diluting the relevance of the information and masking any potential effects of the emotional display. Further studies controlling for that are necessary. Finally, the presence of the owner during the emotional phase and the test may have caused an interference on how dogs perceived the human in terms of being more or less positive, more or less negative. According to Payne et al. (2015) the presence of a person can attenuate the effect of stressful events. In fact, the presence of the owner may function as a safe haven and may play a secure base effect.

Social learning is particularly effective among social animals (Fedurek et al., 2015) and dogs are one of the species that benefit from it (Range et al., 2009). Dogs are capable to obtain, store, and use information through demonstration of people as well as other dogs in observational and manipulative tasks (Range et al., 2009; 2007; Scandurra et al., 2016). At the same time, dogs can discriminate (Nagasawa et al., 2011), categorize (Müller et al., 2015), recognize (Albuquerque et al., 2016), and respond (Albuquerque et al., 2018) to emotional expressions, which allow them to assess the reactions, motivational states and intentions of others. In fact, the ability to perceive the emotions of others is one of the main social regulation mechanisms (Gross, 1998) and domestic dogs possess that as well. Here, we demonstrate that the mechanisms involved in observational social learning must be looked more in depth, since classical ideas of copying or imitation seem to not be likely from recent evidence. Most importantly, emotional cues did not interfere on our subjects' performance, meaning that our hypothesis was not true, at least by using the sort of experimental procedures we have. The emotional display phase did not affect the learning environment, impairing or aiding social learning, or changing the value of the demonstrator and the information she was providing in a relevant way to decrease or increase the speed and the quality of learning. Even though our results do not corroborate the hypotheses raised by our team, they add important aspects to the literature and pave the way for further investigation in the dog cognition and social behavior areas.

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 University of São Paulo Animal Ethics Committee. 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

NA and BR designed the experiment. NA collected the data. FC coded the videos. CS and NA analyzed the data. All authors wrote the manuscript and approved it for publication.

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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.2021.615074/full#supplementary-material

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