



Adjustment in the point-following behaviour of free-ranging dogs – roles of social petting and informative-deceptive nature of cues

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Abstract

Animals of different taxa can read and respond to various human communicative signals. Such a mechanism facilitates animals to acquire social information and helps them react in a context-dependent manner. Dogs have garnered extensive attention owing to their socio-cognitive skills and remarkable sensitivity to human social cues. For example, dogs readily respond to different human pointing gestures to locate hidden food rewards. However, a general inclination towards testing highly socialized pet dogs has resulted in a dearth of information on other sub-populations of dogs. Free-ranging dogs are one of the least socialized dog populations yet exhibit point-following behaviour flexibly. As a consequence of frequent negative interspecific interactions, they are typically wary of unfamiliar humans; thus, contextual recognition of human actions is paramount for these dogs to avoid potential conflict. However, the mechanisms influencing their point-following behaviour remain unidentified. We asked to what extent the informative-deceptive nature of cues and positive human interactions influence the interspecific communicative behaviour of these minimally socialized dogs. Using a point-following experiment with a 2×2 design, we focused on adult free-ranging dogs' behavioural adjustments. Dogs were randomly divided into two groups, with only one receiving brief social petting. Further, informative and deceptive cues were given to separate subsets within each group. Our findings suggest that brief social petting strongly affects the likelihood of free-ranging dogs' point-following tendencies. Dogs who received petting followed the pointing cues regardless of their informative or deceptive nature, whereas dogs who did not receive petting discriminated between informative and deceptive pointing. This study highlights the contribution of positive human interaction and informative-deceptive quality of cues in modulating the behavioural responses of free-ranging dogs in an interspecific communicative context.

Keywords Socio-cognitive skills · Interspecific communication · Human social petting · Point-following · Dogs

Introduction

A wide range of animals, domesticated and non-domesticated, are known to read and respond to human communicative signals like gaze (Macaques—Rosati and Hare 2009; Ravens—Bugnyar et al. 2004; Great apes—Bräuer et al. 2005; Wolves—Range and Virányi 2011; Goats—Kaminski

et al. 2005; Dogs—Téglás et al. 2012) and pointing gestures (Dogs—Miklósi and Soproni 2006; Horses—Maros et al. 2008; Dingoes—Smith and Litchfield 2010; Bats—Hall et al. 2011; Sea lions—Malassis and Delfour 2015; Goats—Nawroth et al. 2020). The presence of such non-verbal communicative skills beyond the confines of phylogenetic relationships has led researchers to investigate their evolutionary origin. In interspecific interactions with humans, animals with such adaptive skills benefit by acquiring social information, which can further help them react in situation-specific manners (Brooks and Meltzoff 2002; Koyasu and Nagasawa 2019; Schaffer et al. 2020; Schrimpf et al. 2020).

Domestic dogs (*Canis lupus familiaris*) are arguably the most studied animal concerning interspecific communication, primarily because of their 'human-like' social skills (Hare and Tomasello 2005). It has been shown that the individual differences in the socio-cognitive domain, especially

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cooperative communicative skills, are more similar between dogs and human toddlers than chimpanzees (MacLean et al. 2017). Such skills in humans and dogs are believed to be an outcome of their convergent evolution (Fitch et al. 2010; Hare and Tomasello 2005; Miklósi et al. 2004). Therefore, dogs might have been selected to cooperate and communicate with humans from a very early age (Salomons et al. 2021). An empirically supported alternate hypothesis suggests the influence of ontogenic experiences instead of genetic predispositions (Udell et al. 2010a). The authors proposed a “Two-stage hypothesis”, stating that sensitivity to human actions in individuals stems from their tendency to accept humans as social companions and subsequent conditioning to follow human limbs. Gácsi et al. (2009), on the other hand, proposed a “Synergistic hypothesis”, suggesting that both evolutionary and epigenetic processes have increased dogs' readiness to attend to humans in social contexts. Although the exact processes by which dogs have acquired those skills are debatable (Marshall-Pescini and Kaminski 2014; Wynne 2021), studies have established pet dogs' remarkable sensitivity to human social cues, primarily related to human pointing gestures (Bräuer et al. 2006; Bray et al. 2021; Miklósi and Soproni 2006; Salomons et al. 2021; Soproni et al. 2001, 2002; Udell et al. 2008). Apart from their readiness to follow human pointing, pet dogs have been shown to blindly follow such cues, ignoring deception (Dwyer and Cole 2018; Kunderly et al. 2010; Petter et al. 2009). For example, pet dogs have been shown to repeatedly follow deceptive cues and visit transparent non-baited containers, thus failing to distrust the deceivers (Dwyer and Cole 2018). An argument can be made that pet dogs are already highly socialized and indirectly conditioned through extensive human interactions. The relatively lower rates of point-following in shelter dogs, who typically are less socialized than pet dogs, supports this argument further (Jarvis and Hall 2020; Udell et al. 2010b). Furthermore, positive human socialization has proved to effectively reduce stress and induce behavioural changes in shelter dogs (Coppola et al. 2006; Hennessy et al. 2006). Recent comparative studies have pointed out the least human socialization levels of free-ranging dogs (Brubaker et al. 2017, 2019; Lazzaroni et al. 2020; Marshall-Pescini et al. 2017). These dogs represent the majority of the world dog population (Hughes and Macdonald 2013; Lord et al. 2013), and yet remain largely understudied. Studying interspecific communication between humans and free-ranging dogs can thus be advantageous for generating valuable scientific knowledge on dog–human relationships and the evolution of socio-cognitive skills in dogs.

Although free-ranging dogs typically do not have “owners”, humans are an integral part of their social interaction dynamics (Bhattacharjee and Bhadra 2020). Despite having a high mortality rate inflicted by humans (Paul et al.

2016), these dogs communicate and interact with humans regularly (Bhattacharjee et al. 2018, 2020a, b), even live and make dens close to human households (Sen Majumder et al. 2016). Nevertheless, like most urban species, they are aversive to making direct contact with unfamiliar humans; however, positive interaction in the form of repetitive and brief social petting has been shown to help build dogs' trust with humans (Bhattacharjee et al. 2017b). Nevertheless, situation-specific responsiveness and plasticity in their behavioural responses are crucial, especially when interacting with unfamiliar humans. The point-following behaviour of free-ranging dogs has been investigated using dynamic proximal, dynamic distal and momentary distal cues (from simple to relatively complex). Spatial co-occurrence of stimuli with the goals (i.e., a small distance between the object and pointing finger) could help guide the behaviour of dogs during dynamic proximal cues, making them easier to follow, contrary to the dynamic and momentary distal cues (Morris 1981). Findings suggest free-ranging dogs' ability to follow simple and complex cues from unfamiliar humans without formal training (Bhattacharjee et al. 2017a, 2019). Researchers found that a higher proportion of dogs followed complex cues than the simple ones at the population level. It was attributed to the fact that these dogs are habituated to humans throwing food away from themselves, thus involving a socio-cultural perspective. As a result, the ‘complex’ cues were thought to be easier to follow than the ‘simple’ cues. Interestingly, adult dogs were found to adjust their point-following behaviour, taking into account the reliability of the human experimenter. In other words, adult dogs were following cues more frequently when getting rewarded than not rewarded in a preceding trial; similarly, they followed cues less frequently when not rewarded in a preceding trial. These results suggest plasticity in the point-following behaviour of free-ranging dogs. However, the decision rules or mechanisms that influence plasticity in the point-following behaviour are not fully understood.

We identified two potential contributing factors—positive human interaction and the informative-deceptive nature of the cues, and investigated their influence on dogs' adjustment in the point-following behaviour. We specifically used dynamic proximal pointing cues (Soproni et al. 2001, 2002) as these dogs were found to be “less successful” at following them than the dynamic and momentary distal cues (Bhattacharjee et al. 2019). We provided a set of dogs with repetitive positive petting (condition—“petting”) while another group received no such human interaction (condition—“non-petting”). Furthermore, from each condition, a subset of dogs was tested with informative cues and another subset with deceptive cues. We predicted that, in general, dogs who received petting would follow human pointing cues more frequently and with shorter latencies than dogs in the non-petting condition. We also predicted that dogs in the petting

condition, unlike non-petting, would ignore deception and continue to follow such cues because of their recent positive interactions with humans. Therefore, in the absence of social petting, we expected dogs to respond in a situation-specific manner towards the informative and deceptive cues.

Materials and methods

(a) Study area and subjects – We randomly selected a total of 111 adult free-ranging dogs, of which 31 dogs did not show any motivation to participate (failed to succeed in familiarization phase); hence the final sample size was 80 (male–female ratio—1:1). Although the exact age of the dogs could not be determined, all of them appeared (by looking at body size and genital structures) to be young adults, i.e. 18–24 months of age or older (Cafazzo et al. 2010). The study was carried out in the following geographic locations—Bengaluru (13°06′ 25″ N, 77°57′ 06″ E), Mohanpur (22°56′ 49″ N, 88°32′ 4″ E), Kalyani (22°58′ 30″ N, 88°26′ 04″ E), and Raiganj (25°61′ 85″ N, 88°12′ 56″ E), India. The study locations can broadly be categorized into urban (Bengaluru, Raiganj, Kalyani) and semi-urban (Mohanpur) areas and had intermediate human movement or flux as conceptualized by a recent study (Bhattacharjee et al. 2020a). We avoided busy and crowded streets, marketplaces, and bus stations for the experiments, as tracking individual dogs is extremely challenging in those areas. Thus, partly residential areas with small markets, roads and shops were sampled (Figure S1). We walked on the streets of a pre-assigned area randomly to locate individual adult free-ranging dogs. Since free-ranging dogs are ubiquitous in Indian streets (Vanak and Gompper 2010), finding a dog was easy. We typically approached dogs when they were not accompanied by conspecifics, e.g., their group members. Furthermore, we avoided testing individuals with awake and attentive group members to limit their potential influence on the behaviour of the subject dogs. The subject dogs and experimenters were not familiar with each other prior to the study. The subject dogs' previous life history was unknown; consequently, it was not possible to quantify their existing relationship with humans. The experiments were conducted at the same locations where the dogs were sighted. We did not see stressful behavioural indicators like tail tucked in between legs, head flat or down, and retracted lips; thus, we assumed that the dogs were sighted in their own territories. Morphological features (coat colour, specific colour patches on the body, scar marks, and body size) were noted to identify and track dogs. We confirmed the sexes of the dogs by observing their genitalia (Morris 2016).

(b) Experimental procedure – One male experimenter (E) was present throughout the study and provided the pointing cues. E was assisted by four volunteers (E_O), each at different

times. We used raw chicken pieces (~8–10 g) as hidden food rewards, and positive social behaviour was provided by brief petting (~10 s) on the dogs' heads. Three opaque plastic bowls (vol=400 ml) and cardboard pieces were used in the experiment. We used a modified but standardized posture while providing the dynamic proximal pointing cue, where E slightly bent down instead of kneeling before a dog (Bhattacharjee et al. 2017a). The distance between the tip of the pointing finger and the bowl was always kept within 0.1 to 0.3 m. The pointing gesture was enacted in full view of a dog, and the arm remained in the pointing position until the choice was made. Each dog was tested over five days (Day 1–Day 5).

Upon sighting a dog, E_O tried to lure him/her and carried out a familiarization phase in the absence of E. Only dogs that succeeded in this phase were considered for further experimentation. The detailed experimental procedure is described below.

(i) One-time familiarization phase—To familiarize dogs with the experimental set-up, E_O carried out this phase on Day 1, with E being out of sight of the subjects. E_O showed and allowed an individual dog to sniff a raw chicken piece, placed it inside an opaque plastic bowl, and covered it with a cardboard piece. E_O put the bowl on the ground at an approximate distance of 1 m from the dog. Video recording of the process was done starting from the bowl's placement and continued for a maximum period of 30 s or until an individual retrieved the food reward, whichever was earlier. Dogs that successfully obtained the food were included in the subsequent phases of the study. As reported, a total of 31 dogs did not approach the experimental set-up and thus failed to succeed in the familiarization phase; these were not included in the study.

(ii) Testing naïve response—Immediately after the familiarization phase, E tested dogs' reactions to dynamic proximal pointing cues (Figure S2). We defined the response of a dog to pointing cues on Day 1 as a naïve response. E put food rewards in two identical but new opaque plastic bowls (each bowl had one food reward inside), covered them with cardboard pieces, and placed them on the ground. Dogs were not allowed to see the process of baiting; thus, we used a single-blind experimental approach. E placed the covered bowls on the ground (approximately 1.2 m away from each other) in a way that they remained equidistant from the focal dog. The approximate distance between the midpoint of the two bowls and the focal dog was 2 m. Additionally, E stood 0.5 m back from the mid-point of the bowls. Once the bowls were placed on the ground, E tried to get the focal dog's attention by clapping softly. After catching the dog's attention, E randomly pointed towards one of the bowls and continued to gaze at the dog throughout the trial. Since the dogs were not confined, E sometimes had to adjust his position along with the bowls, to keep the distances consistent.

Moreover, when dogs approached the set-up before E could provide the cues, the trial was called off, and the bowls were removed immediately. In such instances, E_O distracted the dogs from the experimental set-up while E prepared for a trial repetition.

The whole procedure was video recorded for 30 s or until the focal dog made his/her choice by retrieving the hidden food reward from one of the bowls, whichever was earlier. The content of the unselected bowl was not revealed to the dog afterwards. E_O was present out of the sight of the focal dog to avoid any bias.

(iii) Assignment of conditions and cues – Followed by testing on Day 1, we assigned experimental conditions (petting or non-petting) and types of cues (informative or deceptive) randomly to the dogs. A set of 40 dogs was assigned to the petting condition, while the other set of 40 dogs belonged to the non-petting condition. Furthermore, within both petting and non-petting conditions, a subset of 20 dogs was provided with informative cues, and another subset of 20 dogs received deceptive cues. We kept track of all the dogs. The petting condition dogs were provided with positive social petting on Days 2, 3, and 4. Petting was given for roughly 10 s by E on each of the three consecutive days. Dogs assigned to the non-petting condition did not receive social petting. However, E visited these dogs on Days 2, 3, and 4 to eliminate any potential bias caused by familiarity.

(iv) Testing final response – On Day 5, E tested the final responses of dogs. We used a similar procedure as mentioned in the section ‘Testing naïve response’, except for the following steps—here, E tested dogs in three consecutive trials (5–8 s intervals in between) using either informative or deceptive cues (whichever was assigned earlier). E placed a single food reward in one of the bowls. The other bowl was false-baited by rubbing a piece of chicken on its surface to help control for olfactory cues as far as possible. E either pointed at the baited bowl to provide an informative cue or at the non-baited one to provide a deceptive cue.

As mentioned above, the cue assignment was done randomly, and an individual was tested either with informative or deceptive cues throughout the trials. The bowls' positions were counterbalanced, and the use of right and left pointing hands (always ipsilateral) were randomized. Unlike Day 1, the content of an unselected bowl was revealed to the dogs after completing a trial.

(c) Data coding—A single coder coded all the videos. We coded the point-following responses and latencies to follow. A naïve person blind to the study's purpose coded 20% of the data to check for coder reliability. Reliability was found to be very high (Point-following: Cohen's $k = 1.00$; Latency: Spearman correlation $r_s = 0.89$). Focal dog's uncovering a pointed bowl was considered as a point-following response. Point-following behaviour was coded as a binary variable (followed / not followed).

Latency was defined as the time difference between the presentation of a cue and a dog uncovering a bowl. It was coded as a continuous variable.

(d) Data analysis and statistics – To validate whether the assignment of cues and experimental conditions to the dogs were random, we first conducted a binomial generalized linear model (GLM, Model 1). We used point-following responses of dogs (followed/not followed) on Day 1 as the response variable; cues (informative/deceptive) and experimental conditions (petting/non-petting; note that the different cues and experimental conditions were assigned later) were included as fixed effects. To check for the impact of positive social petting on point-following, we conducted a binomial GLMM (Model 2). Point-following response of dogs was included as response variable while experimental conditions, day of testing (day 1/day 5), and an interaction term of experimental conditions and day of testing were used as fixed effects. To eliminate any potential impact of learning, we used only Trial 1 data of Day 5 in this model. We carried out two binomial GLMMs for the petting (Model 3) and non-petting (Model 4) conditions to investigate the effects of types of cues and trials (Trial 1/Trial 2/ Trial 3) on the point-following responses. We included fixed effects and their interaction terms in both the GLMMs. Sex was included as a control variable in all the statistical models above. Identities of dogs were included as random effects in the GLMMs.

We analyzed latency data in the same way as the point-following responses. In the models, latency was used as the response (continuous) variable (Model 5–8), all other variables remained the same. Before running the models, we checked for the skewness of the data. We found positively skewed data distribution (skewness range: 1.55 – 4.11); Additionally, we found the residual distribution to be non-Gaussian. Therefore, we used Gamma error distribution with ‘‘inverse’’ link functions in the GLM and GLMMs to analyze such a positively skewed continuous variable. Similar to the previous models, we included sex as a control variable in all models and also individual identities in the GLMMs.

The alpha level was 0.05 throughout the statistical analyses. GLM and GLMM analyses were performed using ‘‘lme4’’ package (Bates et al. 2015) of R. Null vs full model comparisons were carried out for all the models. The null models lacked the fixed effects except for the control variable of sex. Post-hoc comparisons (whenever required) were made using ‘‘emmeans’’ package of R (Lenth 2018), and adjusted p values were reported. Residual diagnostics (dispersion, normality, and outlier testing of residuals) of the models were checked using ‘‘DHARMA’’ package of R (Hartig 2020). Statistical analyses were carried out in R Studio (version 3.6.2) (R Development Core Team 2015).

Results

(i) Point-following – We found no significant effects of the experimental conditions (Model 1: $z = -1.168, p = 0.24$) and types of cues (Model 1: $z = -0.660, p = 0.51$) on dogs’ naïve point-following responses on Day 1 (Table S1). Therefore, the assignment of experimental conditions and cues were random and statistically validated.

We found a significant interaction effect of day of testing and experimental conditions (Model 2: $z = -3.453, p < 0.001$, Table S2) on dogs’ point-following responses. Post-hoc analyses revealed that dogs who received petting increased their likelihood of point-following from Day 1 (55%) to Day 5 (97.5%) ($z = -3.307, p < 0.001$, Fig. 1, left panel). However, dogs in the non-petting condition exhibited comparable point-following tendencies on Day 1 (67.5%) and Day 5 (55%) ($z = 1.185, p = 0.63$, Fig. 1, left panel).

Within dogs in the petting condition, we did not find any significant effect of types of cues and trials on dogs’ point-following responses (Model 3, Table S3). Dogs followed informative and deceptive cues comparably across all three trials (Informative: Trial 1 – 95%, Trial 2 – 90%, Trial 3 – 100%; Deceptive: Trial 1 – 100%, Trial 2 – 80%,

Trial 3 – 85%, Fig. 1, right panel). Unlike the petting condition, we found a significant interaction effect of cues and trials in the non-petting condition (Model 4, Table S4). Post-hoc analyses suggest that dogs adjusted their behaviour depending on informative and deceptive cues. A significant increase in dogs’ likelihood of point-following was noticed from Trial 1 (60%) to 2 (95%, $p = 0.04$) and 3 (95%, $p = 0.04$) when given informative cues. On the contrary, dogs who received deceptive cues exhibited a gradual decrease in their point-following responses from Trial 1 (50%) to 2 (25%, $p = 0.19$) and 3 (10%, $p = 0.02$).

(ii) Latency – We did not find any effect of the experimental conditions (Model 5: $t = 0.599, p = 0.55$) and types of cues (Model 5: $t = -1.737, p = 0.08$) on Day 1 latencies (Table S5), further validating our random assignment of experimental conditions and cues.

A significant interaction effect of day of testing and experimental condition was found predicting latencies (Model 6: $t = -6.994, p < 0.001$, Table S6). Post-hoc analyses suggest that dogs in the petting condition approached significantly faster on Trial 1 of Day 5 (2.2 ± 1.01 s) than on Day 1 (4.2 ± 2.58 s), suggesting an effect of social petting ($z = 7.763, p < 0.001$, Fig. 2, left panel). On the other hand, dogs showed comparable latencies on Day 1 (4.55 ± 2.59 s)

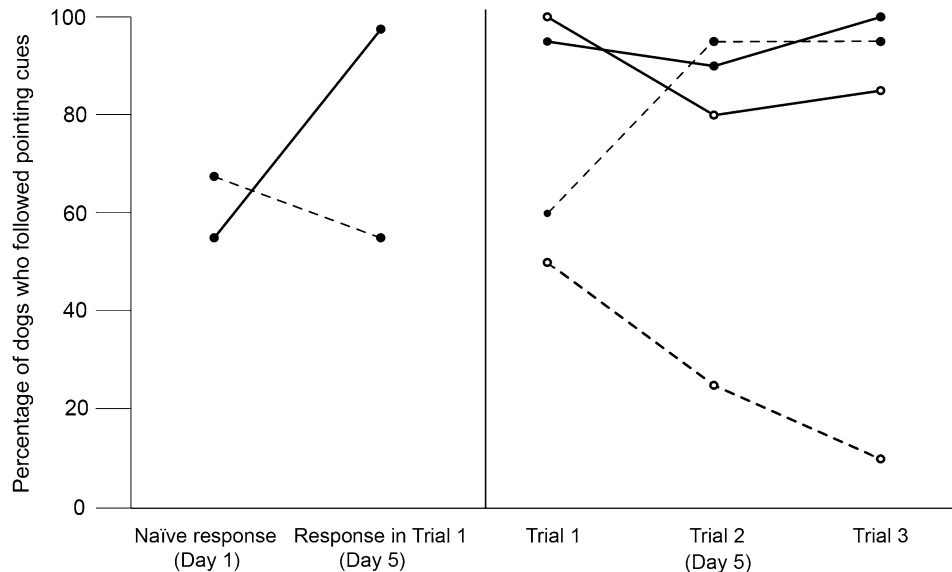


Fig. 1 Figure showing the percentage of dogs who followed human pointing cues in response to different experimental conditions, cues, and trials. Solid and dashed lines indicate dogs’ responses in the petting and non-petting conditions, respectively. Solid and empty circles, respectively, represent informative and deceptive cues (applicable to the right panel only). [Left panel: Solid line – change in dogs’ responses from Day 1 (naïve) to Day 5 (Trial 1) who received social petting (petting); Dashed line – change in dogs’ naïve responses from Day 1 (naïve) to Day 5 (Trial 1) who did not receive social petting

(non-petting); Right panel: Solid line with black circles – change in dogs’ responses who received informative cues from Trials 1 to 3 in the petting condition on Day 5; Solid line with empty circles – change in dogs’ responses who received deceptive cues from Trials 1 to 3 in the petting condition on Day 5; Dashed line with black circles – change in dogs’ responses who received informative cues from Trials 1 to 3 in the non-petting condition on Day 5; Dashed line with empty circles – change in dogs’ responses who received deceptive cues from Trials 1 to 3 in the non-petting condition on Day 5.]

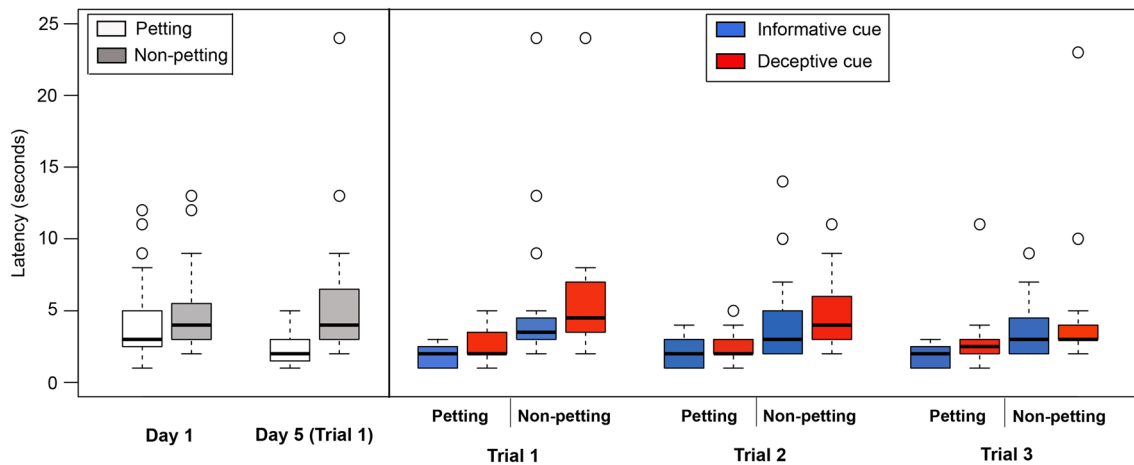


Fig. 2 Box and whisker plot showing the latencies of dogs to approach. Boxes represent the interquartile range, horizontal bars within boxes indicate median values, and whiskers represent the upper range of the data. Circles above whiskers represented non-

significant outliers. The left panel of the figure represents latencies on Day 1 and Day 5 (only Trial 1) from the petting and non-petting conditions. Cue-specific latencies of Day 5 (Trial 1–3) are shown in the right panel

and Day 5 (5.57 ± 4.80 s) in the non-petting condition ($z = -1.417$, $p = 0.48$, Fig. 2, left panel).

In the petting condition, we found no significant effect of cues and trials on dogs' latencies to approach (Model 7, Table S7). Latencies were comparable with informative and deceptive cues across all three trials (Informative: Trial 1 – 1.9 ± 0.78 s, Trial 2 – 2.1 ± 0.96 s, Trial 3 – 1.85 ± 0.81 s; Deceptive: Trial 1 – 2.5 ± 1.14 s, Trial 2 – 2.35 ± 0.93 s, Trial 3 – 2.85 ± 2.10 s, Fig. 2, right panel). No interaction effect of cues and trials was found in the non-petting condition; however, we found an individual effect of trials (Model 8, Table S8). Dogs approached faster in both Trial 2 (4.5 ± 2.66 s; Model 8: $t = 2.005$, $p = 0.04$) and Trial 3 (4.02 ± 3.59 s; Model 8: $t = 3.560$, $p < 0.001$) compared to Trial 1 (5.57 ± 4.80 s) irrespective of informative and deceptive cues (Informative: Trial 1 – 5.25 ± 5.07 s, Trial 2 – 4.2 ± 3.08 s, Trial 3 – 3.5 ± 1.98 s; Deceptive: Trial 1 – 5.9 ± 4.62 s, Trial 2 – 4.8 ± 2.21 s, Trial 3 – 4.55 ± 4.68 s, Fig. 2, right panel).

Discussion

Our results suggest that both positive petting and informative-deceptive content of cues can significantly influence free-ranging dogs' responses to human pointing cues. Dogs exhibited a higher tendency to follow pointing when received social petting, as opposed to no social interactions with the experimenter. Social petting also led dogs in the petting condition to approach and respond faster than their counterparts in the non-petting condition. As predicted, dogs who received petting ignored deceptive cues, failing

to “distrust” the human experimenter. On the other hand, dogs who did not receive petting adjusted their behaviour accordingly, indicating plasticity in their point-following behaviour.

Brief and repetitive social petting, but not food, has been shown to help form free-ranging dogs' trust (i.e., reduced latency, higher proportion of affiliative behaviour, and making physical contact to obtain food) with unfamiliar humans (Bhattacharjee et al. 2017b). The current study provides evidence for the first time that even a brief exposure to positive social interactions can impact free-ranging dogs' interspecific communication with humans significantly. However, it would be difficult to ascertain the exact underlying mechanism(s) with the current experimental design. In other words, whether dogs indeed formed trust or this was an outcome of associative learning, should be carefully studied in the future. Nevertheless, such short exposure modulated behavioural responses in these minimally socialized dogs even outside their critical socialization period (4–10 months; Freedman et al. 1961). Following cues from a trustworthy human being can be advantageous for dogs to potentially secure food and/or shelter without any immediate threat. Free-ranging dogs are known to assess human intentions by postures and attentional states (Bhattacharjee et al. 2018, 2020b; Brubaker et al. 2019). Similar socio-cognitive skills might help them distinguish between a trustworthy and a neutral human being. Also, a person's likelihood of harming dogs (e.g., beating and chasing) is very low when he/she actively pet or make positive social contact with dogs (personal observation).

The adjustment of point-following by the non-petting condition dogs can be attributed to their ability to assess human reliability. Such an adjustment happened gradually,

especially when dogs were provided with deceptive cues; a significant change in point-following was noticed only between Trial 1 and 3. Dogs without positive social interactions were more likely to follow pointing information on subsequent trials when given informative cues. Therefore, in the absence of immediate positive interactions, these dogs do not blindly follow cues from unfamiliar yet neutral humans and might rely on information from repeated such interactions. These results demonstrate free-ranging dogs' ability to follow human communicative cues flexibly using conditional strategies.

Dogs' significantly shorter latencies in the petting than the non-petting condition also provide evidence for our hypothesis, highlighting a key influence of positive social interaction. However, in the absence of petting, we found dogs reacting faster in the later trials of the non-petting condition (irrespective of cue types). Although our results can be explained primarily by free-ranging dogs' remarkable skills to assess human reliability, a potential influence of familiarity and habituation cannot be disregarded. It is known that relatively little exposure is sufficient to socialize and habituate dogs (Scott and Marston 1950); therefore, repeated interactions between the human experimenter and dogs in our study might have impacted dogs' responsiveness to some extent. However, we controlled for the familiarity of the human experimenter in our study by visiting even dogs who did not receive any positive social interactions, making the comparisons consistent. Nevertheless, repeatedly encountering the same experimenter throughout the study period and not receiving any adverse interactions can translate into habituation. It is important to note that we kept the number of experimental days and trials as minimal as possible to lessen the potential effects of habituation. Future studies with different methodological approaches could be conducted to disentangle the effects of habituation from dogs' socio-cognitive skills. Additionally, it would also be interesting to explore whether the behavioural responses of the subject dogs have long-term consistency.

In conclusion, our study highlights the impact of immediate experiences with humans in dogs' behavioural adjustments in a communicative context. Considering the larger picture, such findings support the idea that ontogenic experiences can impact dogs' socio-cognitive skills like human point-following (Udell et al. 2010a; Udell and Wynne 2010; Wynne et al. 2008). At the same time, our results show that minimally socialized free-ranging dogs could follow human pointing cues, apparently indicating a potential influence of domestication (Gácsi et al. 2009; Hare and Tomasello 2005). However, it is inappropriate to conclude whether domestication indeed shaped such skills, primarily because of a significant confounding factor present in this study. It is known that humans play a central role in the social interaction networks of free-ranging dogs (Bhattacharjee and Bhadra

2020). Therefore, even though free-ranging dogs are minimally socialized at the population level, they still interact frequently with humans. Thus, the lack of information on the subject dogs' existing socialization levels with humans prevented us from claiming an effect of domestication, though it should be noted that any training or familiarization with the experimenter was absent for all the subject dogs. This study identifies two significant factors, namely socialization through positive human interactions and information content of cues that influence the interspecific communicative behaviour of free-ranging dogs with humans. This all more highlights how even short interactions between an unfamiliar human and a free-ranging dog on the street can be instrumental in building long-term positive attachment between them, thus providing interesting insights into the process of domestication of dogs.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10071-021-01573-6>.

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Declarations

Conflict of interest We declare no conflict of interests.

Ethical approval All procedures used were in accordance with the ethical standards of the Indian Institute of Science Education and Research Kolkata (approval no. 1385/ac/10/CPCSEA). All meat (raw chicken) used in the experiments were fresh and fit for human consumption.

References

- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw.* <https://doi.org/10.18637/jss.v067.i01>
- Bhattacharjee D, Bhadra A (2020) Humans dominate the social interaction networks of urban free-ranging dogs in India. *Front Psychol.* <https://doi.org/10.3389/fpsyg.2020.02153>
- Bhattacharjee D, Narendradev N, Gupta S et al (2017a) Free-ranging dogs show age related plasticity in their ability to follow human pointing. *PLoS ONE* 12:e0180643. <https://doi.org/10.1371/journal.pone.0180643>
- Bhattacharjee D, Sau S, Das J, Bhadra A (2017b) Free-ranging dogs prefer petting over food in repeated interactions with unfamiliar humans. *J Exp Biol* 220:4654–4660. <https://doi.org/10.1242/jeb.166371>

- Bhattacharjee D, Sau S, Bhadra A (2018) Free-ranging dogs understand human intentions and adjust their behavioral responses accordingly. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2018.00232>
- Bhattacharjee D, Mandal S, Shit P et al (2019) Free-ranging dogs are capable of utilising complex human pointing cues. *Front Psychol*. <https://doi.org/10.3389/fpsyg.2019.02818>
- Bhattacharjee D, Sarkar R, Sau S, Bhadra A (2020a) Sociability of Indian free-ranging dogs (*Canis lupus familiaris*) varies with human movement in urban areas. *J Comp Psychol*. <https://doi.org/10.1037/com0000241>
- Bhattacharjee D, Sau S, Bhadra A (2020b) “Bolder” together — response to human social cues in groups of free-ranging dogs. *Behaviour* 157:363–384. <https://doi.org/10.1163/1568539X-bja1005>
- Bräuer J, Call J, Tomasello M (2005) All great ape species follow gaze to distant locations and around barriers. *J Comp Psychol* 119:145–154. <https://doi.org/10.1037/0735-7036.119.2.145>
- Bräuer J, Kaminski J, Riedel J et al (2006) Making inferences about the location of hidden food: Social dog, causal ape. *J Comp Psychol* 120:38–47. <https://doi.org/10.1037/0735-7036.120.1.38>
- Bray EE, Gruen ME, Gnanadesikan GE et al (2021) Dog cognitive development: a longitudinal study across the first 2 years of life. *Anim Cogn* 24:311–328. <https://doi.org/10.1007/s10071-020-01443-7>
- Brooks R, Meltzoff AN (2002) The importance of eyes: how infants interpret adult looking behavior. *Dev Psychol* 38:958–966. <https://doi.org/10.1037/0012-1649.38.6.958>
- Brubaker L, Dasgupta S, Bhattacharjee D et al (2017) Differences in problem-solving between canid populations: Do domestication and lifetime experience affect persistence? *Anim Cogn* 20:717–723. <https://doi.org/10.1007/s10071-017-1093-7>
- Brubaker L, Bhattacharjee D, Ghaste P et al (2019) The effects of human attentional state on canine gazing behaviour: a comparison of free-ranging, shelter, and pet dogs. *Anim Cogn*. <https://doi.org/10.1007/s10071-019-01305-x>
- Bugnyar T, Stöwe M, Heinrich B (2004) Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceed Royal Soc B Biol Sci* 271:1331–1336. <https://doi.org/10.1098/rspb.2004.2738>
- Cafazzo S, Valsecchi P, Bonanni R, Natoli E (2010) Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behav Ecol*. <https://doi.org/10.1093/beheco/arq001>
- Coppola CL, Grandin T, Enns RM (2006) Human interaction and cortisol: Can human contact reduce stress for shelter dogs? *Physiol Behav* 87:537–541. <https://doi.org/10.1016/j.physbeh.2005.12.001>
- Dwyer C, Cole MR (2018) Domesticated dogs (*Canis familiaris*) tend to follow repeated deceptive human cues even when food is visible. *Learn Behav* 46:442–448. <https://doi.org/10.3758/s13420-018-0356-8>
- Fitch WT, Huber L, Bugnyar T (2010) Social cognition and the evolution of language: constructing cognitive phylogenies. *Neuron* 65:795–814. <https://doi.org/10.1016/j.neuron.2010.03.011>
- Freedman DG, King JA, Elliot O (1961) Critical period in the social development of dogs. *Science* 133:1016–1017. <https://doi.org/10.1126/science.133.3457.1016>
- Gácsi M, Borbála G, Zsófia V et al (2009) Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. *PLoS ONE* 4:e6584. <https://doi.org/10.1371/journal.pone.0006584>
- Hall NJ, Udell MAR, Dorey NR et al (2011) Megachiropteran bats (pteropus) utilize human referential stimuli to locate hidden food. *J Comp Psychol* 125:341–346. <https://doi.org/10.1037/a0023680>
- Hare B, Tomasello M (2005) Human-like social skills in dogs? *Trends Cognit Sci*. <https://doi.org/10.1016/j.tics.2005.07.003>
- Hartig F (2020) DHARMA: Residual diagnostics for hierarchical regression models. In: The comprehensive R archive network. <http://florianhartig.github.io/DHARMA/>
- Hennessy MB, Morris A, Linden F (2006) Evaluation of the effects of a socialization program in a prison on behavior and pituitary–adrenal hormone levels of shelter dogs. *Appl Anim Behav Sci* 99:157–171. <https://doi.org/10.1016/j.applanim.2005.09.011>
- Hughes J, Macdonald DW (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biol Conserv* 157:341–351. <https://doi.org/10.1016/j.biocon.2012.07.005>
- Jarvis T, Hall NJ (2020) Development of point following behaviors in shelter dogs. *Learn Behav* 48:335–343. <https://doi.org/10.3758/s13420-020-00415-8>
- Kaminski J, Riedel J, Call J, Tomasello M (2005) Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Anim Behav*. <https://doi.org/10.1016/j.anbehav.2004.05.008>
- Koyasu H, Nagasawa M (2019) Recognition of directed-gaze from humans in cats. *Japanese J Animal Psychol* 69:27–34. <https://doi.org/10.2502/janip.69.2.3>
- Kundey SMA, Colledge H, Arbutnot J et al (2010) Domesticated dogs’ (*Canis familiaris*) response to dishonest human points. *Int J Compar Psychol* 23(2):201–215
- Lazzaroni M, Range F, Backes J et al (2020) The effect of domestication and experience on the social interaction of dogs and wolves with a human companion. *Front Psychol*. <https://doi.org/10.3389/FPSYG.2020.00785>
- Lenth RV (2018) Emmeans: Estimated marginal means, aka least-squares means. R package version 1.1. In: <https://CRAN.R-project.org/package=emmeans>. <https://cran.r-project.org/web/packages/lsmmeans/vignettes/using-lsmmeans.pdf>
- Lord K, Feinstein M, Smith B, Coppinger R (2013) Variation in reproductive traits of members of the genus *Canis* with special attention to the domestic dog (*Canis familiaris*). *Behavioural Processes*
- MacLean EL, Herrmann E, Suchindran S, Hare B (2017) Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Anim Behav* 126:41–51. <https://doi.org/10.1016/j.anbehav.2017.01.005>
- Malassis R, Delfour F (2015) Sea lions’ (*Zalophus californianus*) use of human pointing gestures as referential cues. *Learn Behav* 43:101–112. <https://doi.org/10.3758/s13420-014-0165-7>
- Maros K, Gácsi M, Miklósi Á (2008) Comprehension of human pointing gestures in horses (*Equus caballus*). *Anim Cogn* 11:457–466. <https://doi.org/10.1007/s10071-008-0136-5>
- Marshall-Pescini S, Rao A, Virányi Z, Range F (2017) The role of domestication and experience in “looking back” towards humans in an unsolvable task. *Sci Rep*. <https://doi.org/10.1038/srep46636>
- Marshall-Pescini S, Kaminski J (2014) The Social Dog. In: *The Social Dog*. Elsevier, pp 3–33
- Miklósi Á, Soproni K (2006) A comparative analysis of animals’ understanding of the human pointing gesture. *Anim Cogn* 9:81–93. <https://doi.org/10.1007/s10071-005-0008-1>
- Miklósi Á, Topál J, Csányi V (2004) Comparative social cognition: what can dogs teach us? *Anim Behav* 67:995–1004. <https://doi.org/10.1016/j.anbehav.2003.10.008>
- Morris RGM (1981) Spatial localization does not require the presence of local cues. *Learn Motiv* 12:239–260. [https://doi.org/10.1016/0023-9690\(81\)90020-5](https://doi.org/10.1016/0023-9690(81)90020-5)
- Morris D (2016) *Dogwatching: The Essential Guide to Dog Behaviour*, illustrate. Random House, 2016, London, UK
- Nawroth C, Martin ZM, McElligott AG (2020) Goats follow human pointing gestures in an object choice task. *Front Psychol*. <https://doi.org/10.3389/fpsyg.2020.00915>

- Paul M, Sen Majumder S, Sau S et al (2016) High early life mortality in free-ranging dogs is largely influenced by humans. *Sci Rep* 6:19641. <https://doi.org/10.1038/srep19641>
- Petter M, Musolino E, Roberts WA, Cole M (2009) Can dogs (*Canis familiaris*) detect human deception? *Behav Proc* 82:109–118. <https://doi.org/10.1016/j.beproc.2009.07.002>
- R Development Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>. R Foundation for Statistical Computing, Vienna, Austria
- Range F, Virányi Z (2011) Development of gaze following abilities in wolves (*Canis lupus*). *PLoS ONE* 6:e16888. <https://doi.org/10.1371/journal.pone.0016888>
- Rosati AG, Hare B (2009) Looking past the model species: diversity in gaze-following skills across primates. *Curr Opin Neurobiol* 19:45–51. <https://doi.org/10.1016/j.conb.2009.03.002>
- Salomons H, Smith KCM, Callahan-Beckel M et al (2021) Cooperative communication with humans evolved to emerge early in domestic dogs. *Curr Biol*. <https://doi.org/10.1016/j.cub.2021.06.051>
- Schaffer A, Caicoya AL, Colell M et al (2020) Gaze following in ungulates: domesticated and non-domesticated species follow the gaze of both humans and conspecifics in an experimental context. *Front Psychol*. <https://doi.org/10.3389/fpsyg.2020.604904>
- Schrimpf A, Single M-S, Nawroth C (2020) Social referencing in the domestic horse. *Animals* 10:164. <https://doi.org/10.3390/ani10010164>
- Sen Majumder S, Paul M, Sau S, Bhadra A (2016) Denning habits of free-ranging dogs reveal preference for human proximity. *Sci Rep*. <https://doi.org/10.1038/srep32014>
- Smith BP, Litchfield CA (2010) Dingoes (*Canis dingo*) can use human social cues to locate hidden food. *Anim Cogn* 13:367–376. <https://doi.org/10.1007/s10071-009-0287-z>
- Soproni K, Miklósi Á, Topál J, Csányi V (2001) Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *J Comp Psychol*. <https://doi.org/10.1037/0735-7036.115.2.122>
- Soproni K, Miklósi Á, Topál J, Csányi V (2002) Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *J Comp Psychol* 116:27–34. <https://doi.org/10.1037/0735-7036.116.1.27>
- Téglás E, Gergely A, Kupán K et al (2012) Dogs' gaze following is tuned to human communicative signals. *Curr Biol* 22:209–212. <https://doi.org/10.1016/j.cub.2011.12.018>
- Udell MAR, Wynne CDL (2010) Ontogeny and phylogeny: both are essential to human-sensitive behaviour in the genus *Canis*. *Anim Behav* 79:e9–e14. <https://doi.org/10.1016/j.anbehav.2009.11.033>
- Udell MAR, Giglio RF, Wynne CDL (2008) Domestic dogs (*Canis familiaris*) use human gestures but not nonhuman tokens to find hidden food. *J Comp Psychol* 122:84–93. <https://doi.org/10.1037/0735-7036.122.1.84>
- Udell MAR, Dorey NR, Wynne CDL (2010a) What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biol Rev* 85:327–345. <https://doi.org/10.1111/j.1469-185X.2009.00104.x>
- Udell MAR, Dorey NR, Wynne CDL (2010b) The performance of stray dogs (*Canis familiaris*) living in a shelter on human-guided object-choice tasks. *Anim Behav*. <https://doi.org/10.1016/j.anbehav.2009.12.027>
- Vanak AT, Gompper ME (2010) Interference competition at the landscape level: the effect of free-ranging dogs on a native meso-carnivore. *J Appl Ecol* 47:1225–1232. <https://doi.org/10.1111/j.1365-2664.2010.01870.x>
- Wynne CDL, Udell MAR, Lord KA (2008) Ontogeny's impacts on human–dog communication. *Anim Behav* 76:e1–e4. <https://doi.org/10.1016/j.anbehav.2008.03.010>
- Wynne CDL (2021) Dogs' (*Canis lupus familiaris*) behavioral adaptations to a human-dominated niche: A review and novel hypothesis. In: *Advances in the Study of Behavior*. pp 97–162

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