Free-ranging dogs understand human intentions and adjust their behavioral responses accordingly

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12 ABSTRACT

Domestic dogs (*Canis lupus familiaris*) are remarkably sensitive and responsive while 13 interacting with humans. Pet dogs are known to have social skills and abilities to display 14 15 situation-specific responses, but there is lack of information regarding free-ranging dogs which constitute majority of the world's dog population. Free-ranging dogs found in most of 16 the developing countries interact constantly with familiar and unfamiliar humans receiving 17 18 both positive and negative behavior. Thus, understanding human intentions and subsequent behavioral adjustments are crucial for dogs that share habitats with humans. Here we 19 subjected free-ranging dogs to different human social communicative cues (friendly and 20 21 threatening – low and high), followed by a food provisioning phase and tested their responsiveness. Dogs exhibited higher proximity seeking behavior as a reaction to friendly 22 gesture whereas, they were prompted to maintain distance depending on the impact of the 23 threatening cues. Interestingly, only the high-impact threatening showed to have a persistent 24 25 effect which also remained during the subsequent food provisioning phase. An elevated approach in the food provisioning phase elicited the dependency of free-ranging dogs on 26 humans for sustenance. Our findings suggest that free-ranging dogs demonstrate behavioral 27 28 plasticity on interacting with humans; which provides significant insights into the

29 establishment of the dog-human relationship on streets.

30

31 Keywords: Free-ranging dogs, Human intentions, Communication, Behavioral plasticity,

- 32 Dog-human relationship.
- 33

34 INTRODUCTION

35 Recent trends in research on interspecific interactions have unveiled several important

36 aspects regarding the interplay of the component species. Investigating the eco-ethology of

37 one component species and its trajectories can provide adequate information on the other

- 38 (Bertness and Callaway, 1994; Thompson, 1999). Human-animal interaction is one such field
- 39 that attracts researchers to find solutions for evolving problems like human-animal conflict,

40 spread of zoonoses, uncontrolled population growth of unwanted species, etc. In the recent

- times, studies on human-animal interactions have enabled us to apprehend evolutionary
- 42 processes like domestication (Hare et al., 2002; Miklósi and Soproni, 2006). Such scientific

43 investigations, coupled with comparative analyses, also helped us understand the

44 functionality of behaviors and communicative intents of species. As the first domesticated

45 species, dogs have spent a considerably long period of time socially interacting with humans

46 (Larson et al., 2012; Morey, 2006; Perri, 2016). Thus, exploring the dog-human interaction

47 paradigm, is specifically helpful to analyse the underlying dynamics of the domestication

48 process that enabled the transition of wolf-like ancestors to man's best friend.

Domesticated dogs interact with humans regularly and possess social abilities to respond to 49 50 various human actions (Hare and Tomasello, 2005; Miklósi and Soproni, 2006). Dogs are highly sensitive to human communicative cues like pointing, touching, body orientation etc. 51 and in utilising such cues to find hidden rewards such as food (Hare et al., 2002; Miklósi and 52 53 Soproni, 2006). It has been suggested that domestication played a pivotal role in the 54 development of human-like social skills in dogs (Hare and Tomasello, 2005). At the same time, substantial evidence for the importance of life history and ontogenic experience with 55 56 humans in the development of the dog-human relationship is also present (Dorey et al., 2010; Wynne et al., 2008). Dogs have been shown to flexibly adjust their behavior in several 57 interactive instances with humans such as, avoiding pointing cues provided by "unreliable 58 59 humans" (Takaoka et al., 2015), following pointing cues only on being rewarded in a 60 preceding trial, thereby showing the ability to adjust behavioral responses (Bhattacharjee et al., 2017a) etc. One study also confirmed dogs' understanding of human attentional states, 61 suggesting the fact that dogs can specifically ask for help when a human is paying attention to 62 it (Miklósi et al., 2000). Dogs have been shown to give emphasis on human body and face 63 while decoding intentions (Nagasawa et al., 2011). Vas et al. (2005) found that pet dogs can 64 differentiate between friendly and threatening cues provided by an unfamiliar human and can 65 66 display situation-relevant behavior. The same study also reported breed specific differences of dogs' responsiveness due to varying levels of sensitivity towards humans. Except for one 67 study mentioned above, all the other studies explored behavioral plasticity in pet dogs and 68 69 hence is not representative of dogs that are not under the direct supervision, and thereby 70 influence, of humans.

Free-ranging dogs that are primarily present in the developing countries make up almost 80% 71 72 of the world's dog population (Boitani and Ciucci, 1995; Hughes and Macdonald, 2013). However, studies are significantly lacking and insufficient with these dogs. They are partially 73 dependent on humans for their sustenance, but their activities are not directly controlled by 74 humans (Bhadra et al., 2016; Sen Majumder et al., 2014; Paul et al., 2016). Unlike pet dogs, 75 76 the free-ranging subpopulation receive both positive and negative human influences; humans play the most significant role in mortality of these dogs (Paul et al., 2016), while also being 77 78 the primary provider of food. This particular difference, along with other ecological 79 parameters pertaining to survival (competition for food, inter-group dynamics etc.) make free-ranging dogs different from pets. The interaction between free-ranging dogs and humans 80 on the streets are quite complex and dynamic. They usually avoid human contact but can 81 form strong bonds over repeated positive interactions with unfamiliar humans (Bhattacharjee 82 et al., 2017b). Additionally, they need to understand and decipher human intentions clearly. A 83 84 recent study showed that very young pups of free-ranging dogs follow simple human pointing 85 cues but learn to adjust the behavior when they grow up and start foraging events. A greater risk of negative impact from humans like beating, harassment and threatening are probably 86 the prime reasons for such plasticity in point-following behavior (Bhattacharjee et al., 2017a). 87 88 However, this study does not provide us insights into the dogs' understanding of social cues 89 that are used by humans in day to day interactions with these dogs.

- 90 Here we used three different types of commonly used human social communicative cues
- 91 while interacting with dogs on streets. The cues differed in terms of their actions and
- 92 representations. The friendly cue illustrated an affiliative gesture, while the low and high
- 93 impact threatening cues had negative display of gestures. In addition to the three cues, we
- 94 used a neutral cue as control. We tested the responses of the dogs to the cues and investigated
- 95 the influences in a post-cue food provision phase. We hypothesize that the dogs would enact
- 96 positively upon receiving the friendly cue showing higher proximity and approach behavior.
- 97 Additionally, the dogs would avoid human proximity and adjust their responses flexibly
- 98 according to the impacts of the two threatening cues.

99 MATERIALS AND METHODS

100 Subjects and study area

101 We tested 120 adult, physically fit, solitary free-ranging dogs. Dogs were located randomly in

102 different areas of West Bengal, India (see Supplementary Figure S1) for the experiment -

103 Mohanpur (22°56'49''N and 88°32'4''E), Kalyani (22°58'30"N, 88°26'04"E), Sodepur

104 $(22^{\circ}69'82''N \text{ and } 88^{\circ}38'95''E)$ and Kolkata $(22^{\circ}57'26''N, 88^{\circ}36'39''E)$. Sexes of the dogs

- 105 were determined by observing their genitals. To rule out any possibility of resampling, we
- tested dogs from different locations on different days and photographed each individual to
- 107 collect information on coat color, scar marks and other morphological features.

108 Experimental Procedure

- 109 We used four different experimental conditions pertaining to various social cues in order to
- investigate the response of solitary free-ranging dogs towards an unfamiliar human. We
- tested separate sets of 30 dogs in each of the four experimental conditions. All the
- experimental trials were conducted on the same locations where the focal free-ranging dog
- 113 was found (e.g. streets, markets, residential areas etc.). One piece of raw chicken (10-12g)
- 114 was used as food. The experimenters (E1 and E2) were consistent throughout the study,
- 115 played specific roles and were young males. Video recording was done from a distance using
- a Sony HDR-PJ410 camera mounted on a tripod.
- 117 The experimental conditions comprised of 2 major and 3 minor phases, carried out in the 118 following order (Figure S2) –
- **Attention seeking phase (minor) -** E2 attracted the attention of a solitary dog by making
- very short vocalization for 1-2 seconds (Bhattacharjee et al., 2017a). This step was necessary
 as we found some dogs lying down, resting or dozing. To keep the protocol consistent, E2
 carried out this step in all the four experimental conditions.
- Transition phase (minor) Once the dog was alerted, E2 immediately left the place and
 stood behind the camera, which was kept at a minimum distance of 4.5 m from the dog. E1
 arrived near the position where E2 was initially standing. This whole procedure was
 completed within 10 seconds
- **126** completed within 10 seconds.
- Social cue phase / SCP (major) E1 stood approximately 1.5 m away from the dog, facing
 it. Since the dogs were free-ranging and not on leash, E1 had to adjust his position in order to
 maintain the approximate distance of 1.5 m. After standing at the specified spot, E1 provided
 any of the predetermined social cue for 30 seconds –
- *Friendly Cue (FC)* E1 displayed a positive gesture by bending slightly forward and
 extending both the arms (see Supplementary Movie S1). In India, people use similar
 gestures (sometimes clubbed with positive vocalisations) to provide positive social

rewards to dogs. E1, while providing the social cue, gazed and tried to maintain eyecontact with the dog. E1 did not touch the focal dog deliberately in order to avoid any
potential bias of social contact.

- Low impact threatening (LIT) E1 raised one of his hands (counterbalanced) and gazed at the dogs (see Supplementary Movie S2). The cue differed from FC in having a negative display of human gesture. People on the streets often raise one of their hands to scare, threaten or shoo away dogs. We have adopted the same gesture in our protocol to investigate the effects and associated responses.
- 142
- *High impact threatening (HIT)* This phase differed from LIT in terms of impact. Here
 E1 used a 0.45 m long solid wooden stick in his hand (counterbalanced) while providing
 the gesture (see Supplementary Movie S3). E1 had to hide the wooden stick in the
 transition phase before enacting the gesture.
- 147
- *Neutral Cue (NC)* Here, E1 stood in a neutral posture and looked straight ahead and did not enact any gesture.

Food transfer phase (minor) - Immediately after SCP, food was provisioned. E2 came
quickly, handed over the food to E1 and went back to his position behind the camera. The
process was completed within 10 seconds and care was taken to ensure that the focal dog did
not see the transfer of food to E1.

- Food provisioning phase / FPP (major) E1 again adjusted his position to keep the distance
 consistent and placed the food on the ground. The food was placed at a distance of 0.3 m
 from E1, thus at a distance of 1.2 m from the dog. E1 stood in a neutral position after placing
 the food and looked straight ahead, without making eye contact with the dog (see
 Supplementary Movie S4). FPP lasted 30 seconds or until the dog obtained the food,
 whichever was earlier. Food was removed in case a dog did not obtain it.
- Except for the SCP, all the other phases were constant and exactly similar across theexperimental conditions.

162 Data Analysis and statistics

- 163 We coded all the important behaviors relating to the experiment, which have been listed in 164 the ethogram below (**Table 1**).
- 165

166 Table 1 - List of behaviors coded from the videos and their definitions

167

Phase	Behavior		Definition		
	Approach		Subject moved towards E1, distance between E1 and subject was ≤ 0.3 m.		
SCP	No approach	Same position	Distance between E1 and subject was equal to 1.5 m.		
		Distant	Distance between E1 and subject was > 1.5 m.		
	First reaction		The first behaviour observed as a reaction to the social cue – gazing, gazing with tail wag, scared and moving back, no reaction.		

	D	A CC'1'					
	Demeanor (Holistic)	Affiliative	All behaviors towards E1 that are involved in the formation and maintenance of human-dog bonding. Includes attention seeking, proximity seeking, contact seeking, social facilitation, tail wagging, and relaxed posture (Rehn et al., 2013).				
		Aggressive	Agonistic and/or aggressive (dominant or threatening) behavior towards E1. Includes mouthing, biting clothing, jumping up, snapping, growling, baring the teeth, stiff posture, staring and/or "whale-eyeing," high, stiff tail carriage, piloerection (Overall, 2014).				
		Anxious	Anxious or fearful behavior towards E1. Includes shaking (trembling), excessive panting, lip-licking, urination, tail between the legs, running away, flinching, corners of the mouth retracted down and back. May be maintaining distance from the E1 (Lindsay, 2005).				
		Neutral	Demeanour that is not otherwise covered in this ethogram. May include resting and sleeping during the experiment, exploratory behavior not directed at E1 or food (sniffing, digging, chewing, scent rolling), self- care (scratching, licking), or general disinterest in E1.				
	Human Proximity		Distance between E1 and subject was ≤ 0.3 m.				
	Gazing at human		Subject is sitting, standing, or lying and focused on (muzzle turned towards) E1's body or face. Cumulative duration of gazing / looking behavior at E1.				
	Approach		Subject moved towards E1, distance between food and subject was ≤ 0.3 m.				
	No approach	Same position	Distance between food and subject was equal to 1.2 m.				
		Distant	Distance between food and subject was > 1.2 m.				
FPP	Latency		Time taken to obtain the food after its provision on the ground. Valid only for subjects that obtained food.				
	Feeding time (proximity)		Time taken to eat the food in front of E1. Distance of subject and human should be ≤ 0.3 m. Distant (> 0.3 m) feeding or taking food away was not considered.				
	Gazing at human		Same as social cue phase.				

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Shapiro -Wilk tests were used to check for normality of the data. We found the data to be not normally distributed, thus non-parametric tests were carried out. Generalised linear models
(GLM) were performed using "lme4" package of R Studio. AIC values were compared in order to get the best-fitting models. A second coder naïve to the purpose of the study coded 20% of the data to check inter-rater reliability. It was perfect for number of approach (cohen's kappa = 1.00), almost perfect for duration of proximity (cohen's kappa = 0.93),

gazing (cohen's kappa = 0.90) and latency (cohen's kappa = 0.96). The alpha level was 0.05
 throughout the analysis. Post-hoc comparisons were done with Bonferroni correction method

whenever required. Statistical analyses were performed using R (R Development Core Team, 177

2015) and StatistiXL version 1.11.0.0. 178

RESULTS 179

Various statistical tests were carried out for the analysis. Since we have compared parameters 180

- of the major phases in all possible combinations, description of some of the post-hoc 181
- statistical tests were presented in supplementary material to avoid congestion in the main text. 182
- Number approached Dogs approached differently in SCP and FPP of the four conditions 183
- (Contingency χ^2 : $\chi^2 = 10.439$, df = 3, p = 0.015, Figure 1). In the NC condition, initially 4 184
- individuals approached, while the number increased to 17 in FPP, the change being 185
- statistically significant (Goodness of fit χ^2 : $\chi^2 = 8.048$, df = 1, p = 0.005), thereby indicating a 186
- distinct positive impact of food. However, we did not find any difference between the two 187
- phases in the FC condition as dogs equally responded to both positive gestures (25) and food 188 (30), more than expected by chance alone (Goodness of fit χ^2 : $\chi^2 = 0.455$, df = 1, p = 0.50).
- 189 The LIT condition had a very momentary impact as only 1 individual approached in SCP, 190
- while 13 individuals approached in FPP (Goodness of fit χ^2 : $\chi^2 = 10.246$, df = 1, p = 0.001). 191
- Thus, dogs flexibly adjusted their behavior and tended to approach more when food was 192
- 193 provided. Unlike the LIT condition, we found a strong effect of HIT, where none of the
- 194
- individuals approached initially and only 1 (Goodness of fit χ^2 : $\chi^2 = 1.000$, df = 1, p = 0.317) in the later phase, when the food reward was offered. This was suggestive of the dogs' 195
- 196 perception of human intentions based on an immediate encounter.
- 197 We compared the number of approaches across conditions for both SCP and FPP.
- Significantly higher number of dogs approached in SCP in response to FC, as compared to 198
- the NC, LIT and HIT conditions (see Supplementary Table S1). We noticed a marginal 199
- difference between the NC and HIT conditions (see Supplementary Table S1). Additionally, 200
- 201 the number of approaches in the SCP of LIT did not differ from NC and HIT conditions (see
- Supplementary Table S1). 202
- Comparison of the number of approaches among FPP of the four conditions revealed 203 interesting results. Dogs approached significantly more in FC compared to LIT (Goodness of 204 fit χ^2 : $\chi^2 = 6.721$, df = 1, p = 0.010) and HIT (Goodness of fit χ^2 : $\chi^2 = 27.129$, df = 1, p < 205 0.0001), but not NC (Goodness of fit χ^2 : $\chi^2 = 3.596$, df = 1, p = 0.058), again implying the 206 role of the food provisioned. In the HIT condition, the number of dogs that approached was 207 significantly lower than the LIT condition (Goodness of fit χ^2 : $\chi^2 = 10.286$, df = 1, p = 0.001), 208 suggesting an influence of the HIT cue which even surpassed the impact of food. In addition, 209 we also found that the HIT cue differed from NC, but the number of approaches in FPP of 210 LIT and NC conditions were comparable (see Supplementary Table S1). These results 211 together reinforce the idea that dogs were capable of differentiating between the high and low 212 impact threatening cues, and act accordingly, to maximize their chances of obtaining the food 213
- 214 reward while avoiding serious threat.
- *No approach* We calculated the number of individuals in different conditions that did not 215 approach and further divided the numbers in two subcategories - 'same' and 'distant' 216
- position (see Table 1). Here we laid emphasis on the 'distant' position which served as a 217
- 218 correlate of negative impact. Consistent with our hypothesis, we could not see any dog
- running or moving away in the NC and FC conditions, thereby dogs exclusively showed no 219
- approach of 'same position' subcategory. Thus, we analysed the data only from LIT and HIT 220
- conditions. We used the percentage of responses out of the total "no approach" cases for all 221
- the comparisons. 222

52% and 24% of the dogs were distant in SCP and FPP respectively, in the LIT condition 223 (Goodness of fit χ^2 : $\chi^2 = 10.316$, df = 1, p = 0.001, Figure 2). Consistent with this, we also 224 found dogs showing significantly more distant positions in SCP (73%) than the FPP (45%) of 225 the HIT condition (Goodness of fit χ^2 : $\chi^2 = 6.644$, df = 1, p = 0.01, Figure 2). Further 226 comparisons revealed a significant difference between the FPP of LIT and HIT conditions 227 (Goodness of fit χ^2 : $\chi^2 = 6.391$, df = 1, p = 0.011, Figure 2), where higher numbers of dogs 228 stayed at the 'distant' position in the HIT condition. However, we did not find any difference between the SCP of the two conditions (Goodness of fit χ^2 : $\chi^2 = 3.528$, df = 1, p = 0.060). 229 230 First reaction to a social cue – Quantification of the first reaction was important in terms of 231 impact and effect of the social cues. We found that the reactions (see Table 1) were 232 233 distributed differently in the four experimental conditions. In the NC condition, dogs showed varying levels of reactions. 60% of the dogs showed gazing behavior, 10% showed gazing 234 with tail wagging, 30% stayed neutral and displayed no particular reaction. None of the dogs 235 showed a fear response. We found a significant difference among the proportion of 236 individuals showing the different reactions (Goodness of fit χ^2 : $\chi^2 = 25.200$, df = 3, p < 237 0.0001, Figure 3A). Gazing and no reaction were comparable and displayed at a higher rate 238 than other behaviors (see Supplementary Table S1). In the FC condition, we found 80% of 239 the dogs showing gazing with tail wagging as their first reaction, while 20% showed gazing 240 behavior only. No dog showed a fear response, and all dogs responded. Gazing with tail 241 wagging occurred at a significantly higher rate than only gazing behavior (Goodness of fit χ^2 : 242 $\chi^2 = 10.800$, df = 1, p = 0.001, Figure 3B). Except for a single individual, all the dogs reacted 243 in the LIT condition. 60% of the dogs showed fear response to the social cue at a significantly 244 higher rate than both gazing (20%) and gazing with tail wagging (17%) behaviors (Gazing – 245 Goodness of fit χ^2 : $\chi^2 = 6.000$, df = 1, p = 0.014; Gazing with tail wagging – Goodness of fit χ^2 : $\chi^2 = 7.348$, df = 1, p = 0.007, **Figure 3C**). In the HIT condition, 97% of the dogs showed 246 247 fear response when the threatening gesture was enacted, whereas only one individual 248 displayed gazing with tail wagging (Goodness of fit χ^2 : $\chi^2 = 26.133$, df = 1, p < 0.0001, 249 Figure 3D). 250

251 Demeanor - Dogs displayed mostly neutral (43%) and anxious (43%) behaviors in the NC252 condition. Affiliative behaviors were shown at a lower rate than both the neutral and anxious

behaviors (Goodness of fit χ^2 : $\chi^2 = 4.765$, df = 1, p = 0.029, Figure 4). Agonistic or

- aggressive behaviors were absent. Unlike the outcomes in NC, majority of dogs (80%)
- showed affiliative behaviors, rather than neutral (Goodness of fit χ^2 : $\chi^2 = 12.448$, df = 1, p < 0.0001) and anxious behaviors (Goodness of fit χ^2 : $\chi^2 = 21.160$, df = 1, p < 0.0001) in FC.
- Aggression was not observed. In the LIT condition, 57% of the dogs showed anxious
- behaviors, which was higher than all the other three categories (Neutral Goodness of fit
- χ^2 : $\chi^2 = 6.545$, df = 1, p = 0.011; Affiliative Goodness of fit χ^2 : $\chi^2 = 6.545$, df = 1, p = 0.011;
- 260 Aggressive Goodness of fit χ^2 : $\chi^2 = 9.800$, df = 1, p = 0.002). 97% of the dogs showed
- anxious behaviors in HIT condition. However, we did not see a statistical difference between
- the levels of anxious behavior shown in LIT and HIT conditions (Goodness of fit χ^2 : $\chi^2 =$
- 263 3.130, df = 1, p < 0.07).
- 264 *Human proximity* Dogs showed varying levels of proximity to the human experimenter in 265 the different conditions (Kruskal – Wallis test, $\chi^2 = 77.127$, df = 3, p < 0.0001, **Figure 5**).
- 266 Post-hoc pairwise comparisons revealed that the duration of human proximity was higher in
- the FC condition compared to others (see Supplementary **Table S1**). However, we did not
- find any difference between the duration of human proximity in the NC, LIT and HIT
- conditions (see Supplementary **Table S1**), indicating a general avoidance of human proximity
- 270 in free-ranging dogs.

- 271 Gazing GLM analysis revealed that both the LIT and the HIT conditions are significant
- 272 predictors of gazing at E1 in the SCP (**Figure 6**, **Table 2**).

Table 2 – GLM results showing the effect of experimental conditions on gazing behavior in the SCP.

	estimate	Standard error	z- value	Pr(> z)
fixed effects				
Intercept	1.75786	0.07581	23.188	< 2e-16 ***
Condition FC	0.01143	0.10691	0.107	0.914865
Condition HIT	0.43937	0.09722	4.520	6.2e-06 ***
Condition LIT	0.37828	0.09841	3.844	0.000121 ***

275

- 276 Interestingly, in the FPP, we found all the different conditions to be significantly contributing
- to the prediction of the duration of gazing behavior (**Figure 6**, **Table 3**). Dogs gazed the least $(0.46 \pm 1.69 \text{ sec})$ in the FPP of the FC condition.

Table 3 – GLM results showing the effect of experimental conditions on gazing behavior in the FPP.

	estimate	Standard error	z- value	Pr (> z)	
fixed effects					
Intercept	1.1206	0.1043	10.748	< 2e-16 ***	
Condition FC	-1.8827	0.2869	-6.563	5.28e-11 ***	
Condition HIT	0.6315	0.1290	4.894	9.88e-07 ***	
Condition LIT	0.4822	0.1326	3.636	0.000277 ***	

281

282 *Latency and feeding time (food provision phase only)* – Individuals who approached the food,

were considered for the latency comparisons (N = 60). We excluded the HIT condition from

the analysis as only one dog approached and obtained the food reward. Individuals showed

285 different latencies in the three conditions while approaching for the food (Kruskal – Wallis

- test, $\chi^2 = 34.011$, df = 2, p < 0.0001, see Supplementary Figure S3). In the FC condition, the
- 287 dogs approached faster than the NC (Mann Whitney U test, U = 452.000, df1 = 17, df2 = 0.000
- 288 30, p < 0.0001) and LIT (Mann Whitney U test, U = 374.000, df1 = 30, df2 = 13, p < $(10^{-10} 10^{-10})$
- 289 0.0001) conditions. Latencies were comparable in the NC and LIT conditions (Mann –
- 290 Whitney U test, U = 156.500, df1 = 17, df2 = 13, p = 0.053).

291 We found one individual in the FC condition that approached but did not obtain the reward.

Thus, we removed the data point for the analysis of feeding time (N = 59). We found a

- significant difference in feeding time (Kruskal Wallis test, $\chi^2 = 8.366$, df = 2, p = 0.015, see
- 294 Supplementary **Figure S4**). Post-hoc pairwise comparisons further revealed a significant
- difference between feeding times of FC and LIT conditions (Mann Whitney U test, U =

296 298.000, df1 = 29, df2 = 13, p = 0.002). Short feeding time in the LIT condition (2.77 ± 0.72)

sec) compared to FC (4.58 ± 2.02 sec) might be an indication of dogs' insecurities due to

- 298 negative human influence, leading to faster consumption of the food reward. Moreover, we
- did not see any difference between the other two comparisons (see Supplementary Table S1).

300 DISCUSSION

- 301 Our results underline the free-ranging dogs' behavioral plasticity in the context of
- 302 interactions with unfamiliar humans. Dogs adjusted their behavior and showed situation-
- 303 relevant response to the social cues. Overall, they exhibited a tendency to approach more

when food was provisioned compared to the social cue phases, emphasizing the dependence
on humans for sustenance. However, comparable but higher levels of approach in the FC
condition identified an important role of positive social actions from humans, in order to
encourage the initiation of an affiliative relationship. The comparatively higher duration of

- 308 human proximity in the FC further strengthens this statement. The influence of low-impact
- 309 threatening cues was very momentary while the effect of the high-impact threatening cues
- remained even when food was provided. Moreover, dogs avoided the unfamiliar human (E1)
- 311 with a comparatively higher distance in HIT compared to LIT. Thus, dogs were able to
- distinguish between the impacts of the threatening cues and responded accordingly,
- 313 illustrating an optimized strategy. Additionally, the initial reactions and demeanors were
- 314 consistent with the differential approach of dogs to the corresponding cues.

315 Apart from showing affiliative responses in the FC condition, dogs showed adjustments and

- 316 plasticity in their anxious or fearful responses during the threatening cue conditions. Gazing
- behavior in SCP was predicted by LIT and HIT conditions as dogs gazed more, probably
- indicating their hesitant nature to approach and also gauging human intentions. On the other
- hand, FC, LIT and HIT conditions predicted the gazing response in FPP. It is important to
- note that the short duration of gazing at E1 in the FC condition could be the linked to dogs'
- 321 certainty due to affiliative human action. This was also supported by a significantly faster
- approach to the food. Moreover, dogs depicted a tendency to spend more time while feeding
- in the FC condition compared to LIT. Thus, the free-ranging dogs acted very specifically in
- the different conditions displaying a range of social responses that had a high degree of parity
- with the social cue provided in the experiment. .
- 326 Free-ranging dogs live in human dominated environments and heavily depend on humans for 327 food (Bhadra et al., 2016; Bhadra and Bhadra, 2014). Apart from scavenging, they directly beg for food from humans (Bhadra and Bhadra, 2014; Sen Majumder et al., 2014). However, 328 getting or retrieving food items can lead to consequences like beating and harassment, which 329 330 probably have made these dogs opportunistic. In order to avoid negative human impact and maximize the success of getting food, dogs need to identify reliable humans. General 331 avoidance of direct physical contact with unfamiliar humans (Bhattacharjee et al., 2017b) 332 may be a process involved in the same strategy. However, the flexibility might have been 333 achieved by dogs upon receiving positive human reinforcements. For example, adult free-334 ranging dogs have earlier been shown to adjust their point-following behavior based on 335 reliability of unfamiliar humans (Bhattacharjee et al., 2017a). Interestingly, pet dogs have 336 337 been shown to trusting unfamiliar humans in a range of scenarios (see review Hare and 338 Woods, 2013), which could possibly be result of solely positive interspecific interactions. Nevertheless, pets are sensitive to behaviors of strangers (Vas et al., 2005), consistent with 339
- 340 the results of this study.
- 341 Dogs' differential and situation-specific approach behaviors can be explained by early social
- interactions with humans (Fox and Stelzner, 1966). The role of domestication is also
- 343 undeniable, which facilitated dogs' understanding and sensitivity towards human social cues.
- 344 It has been shown that even hand-reared wolves (*Canis lupus*), being the closest
- ancestors of modern day dogs failed to adjust behaviors while interacting with humans in
- ambiguous situations (Bradshaw and Nott, 1995). Thus, an interplay of domestication and
- factors like living environment and experience with humans might be the basis of the overalloutcomes.
- The current experimental design only evaluates dogs' understanding and sensitivity of human social actions. One potential short-coming of the study was not being able to track individuals and failing to incorporate factors like frequency of positive and negative interactions with

- 352 humans in their daily lives. Follow-up studies in different geographic regions with varying
- 353 levels of human influences could be done to see the larger picture. On the brighter side, this
- study has helped to identify a key element in the ecology of the dog-human relationship, the
- ability of the dogs to assess a social cue (and thus intent) of unfamiliar humans, which
- explains why dogs are one of the most successful species in sharing the same niche withhumans.
- 358

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437 AUTHOR CONTRIBUTIONS

- 438 DB and AB conceived and designed the study. DB and SS performed the field experiments as
- 439 E1 and E2 respectively. DB coded the videos and analysed the data. The initial draft was
- 440 written by DB and later reviewed and edited by AB. AB supervised the work. All authors
- 441 gave final approval for publication.
- 442

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453 CONFLICT OF INTEREST STATEMENT

- 454 The authors declare no competing or financial interests.
- 455
- 456 Figure legends -
- **Figure 1. Number of approaches.** Bar graph showing the number of approaches in the SCP and FPP of the four experimental conditions – NC, FC, LIT and HIT. Number of dogs that approached varied between the phases across the conditions (Contingency χ^2 : $\chi^2 = 10.439$, df z = 3, p = 0.015). Asterisks indicated significant differences. The dotted line indicated the
- 461 chance level (50%).

Figure 2. Percentage of distant position out of "no approach". Bar graph showing the percentage of dogs that showed distant position out of "no approach" in the SCP and FPP of LIT and HIT conditions. Dogs showed significantly more distant positions in both the SCP compared to FPP of LIT (Goodness of fit χ^2 : $\chi^2 = 10.316$, df = 1, p = 0.001) and HIT (Goodness of fit χ^2 : $\chi^2 = 6.644$, df = 1, p = 0.01) conditions. Asterisks indicated significant

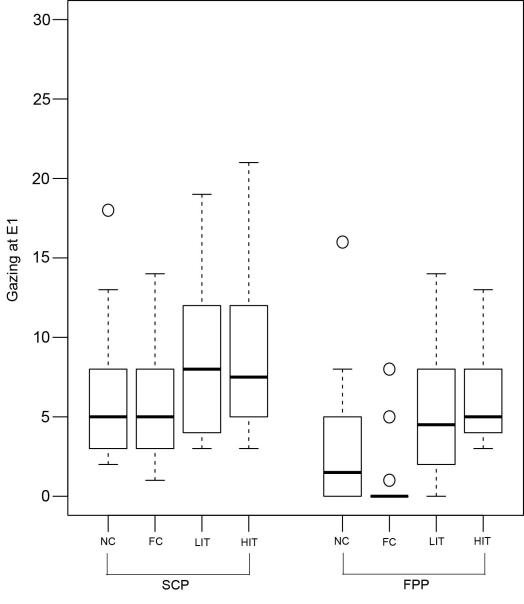
467 differences.

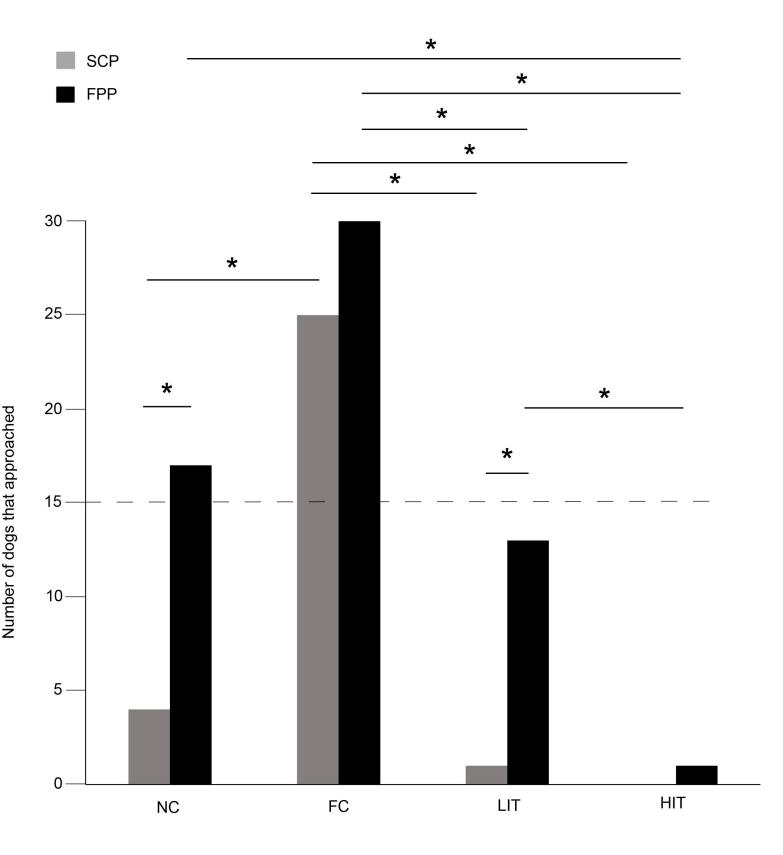
468 Figure 3. First reaction to social cue. Pie charts showing the first reaction (behaviors) to

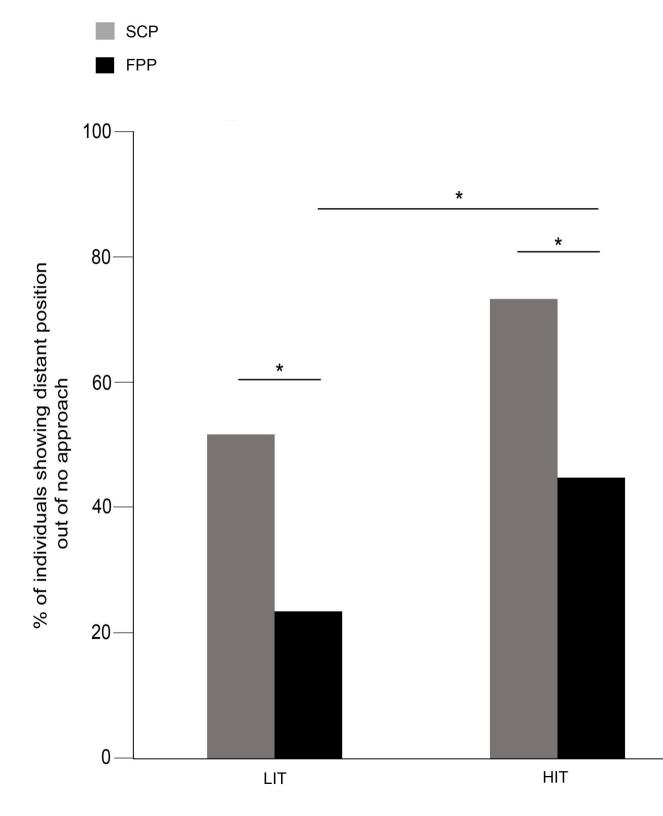
- 469 social cues. (A) Distribution of behavioral responses in NC condition, (B) Distribution of
- 470 behavioral responses in FC condition, (C) Distribution of behavioral responses in LIT
- 471 condition, (D) Distribution of behavioral responses in HIT condition.
- 472 Figure 4. Demeanours (Holistic). Stacked bar graph showing the demeanours of dogs in
 473 SCP of NC, FC, LIT and HIT conditions.

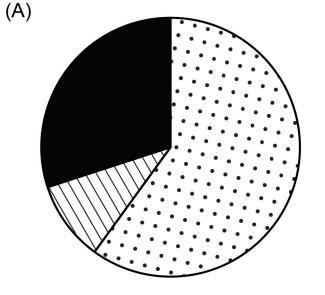
- 474 **Figure 5. Duration of human proximity.** Box and whisker plot illustrating the duration of
- human proximity of dogs in SCP of NC, FC, LIT and HIT condition. Dog showed
- significantly higher proximity to E1 in the FC (12.43±9.54 sec) than in other conditions.
- 477 Boxes represent interquartile range, horizontal bars within boxes indicate median values, and
- 478 whiskers represent the upper range of the data. "a" and "b" indicate significant differences.
- 479 **Figure 6. Duration of gazing.** Box and whiskers plot showing the duration of gazing at E1
- 480 in SCP and FPP of NC, FC, LIT and HIT conditions. Boxes represent interquartile range,
- 481 horizontal bars within boxes indicate median values, and whiskers represent the upper range482 of the data.

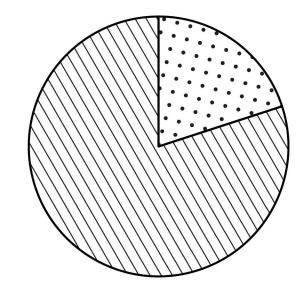
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(B)

