

RESEARCH ARTICLE

Free-ranging dogs prefer petting over food in repeated interactions with unfamiliar humans

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ABSTRACT

Dogs (*Canis lupus familiaris*) are the first species to have been domesticated and, unlike other domesticated species, they have developed a special bond with their owners. The ability to respond to human gestures and language, and the hypersocial behaviours of dogs are considered key factors that have led them to become man's best friend. Free-ranging dogs provide an excellent model system for understanding the dog–human relationship in various social contexts. In India, free-ranging dogs occur in all possible human habitations. They scavenge among garbage, beg for food from humans, give birth in dens close to human habitations, and establish social bonds with people. However, there is ample dog–human conflict on the streets, leading to morbidity and mortality of dogs. Hence, the ability to assess an unfamiliar human before establishing physical contact could be adaptive for dogs, especially in the urban environment. We tested a total of 103 adult dogs to investigate their response to immediate social and long-term food and social rewards. The dogs were provided a choice of obtaining food either from an experimenter's hand or the ground. The dogs avoided making physical contact with the unfamiliar human. While immediate social reward was not effective in changing this response, the long-term test showed a strong effect of social contact. Our results revealed that these dogs tend to build trust based on affection, not food. This study provides significant insights into the dynamics of dog–human interactions on the streets and subsequent changes in behaviour of dogs through the process of learning.

KEY WORDS: *Canis lupus familiaris*, Social contact, Dog–human relationship, Learning

INTRODUCTION

Living in close proximity with humans can have several adaptive advantages for animals, while posing challenges for survival at the same time. Human habitations can be good sources for food, shelter and protection; and many species of animals, from insects to mammals are known to have adapted to co-habiting with humans, as pests, parasites, commensals and domesticates (Castillo et al., 2003; Pocock et al., 2004; Vannier-Santos and Lenzi, 2011). The changing landscape of human habitation, from more rural to more urban over the past decades, has led to an increasing interest in urban ecosystems (Alberti et al., 2008; McIntyre et al., 2008; Pickett et al., 2008). Most of the non-domesticated species that adapt to the urban environment present interesting case studies to understand how they


resolve issues of conflict with humans while exploiting new niches created in these human-dominated landscapes. This question is all the more interesting for species like birds and mammals, in which decision making might be influenced by their experiences from interactions with humans in the urban space (Ditchkoff et al., 2006; Maklakov et al., 2011; White et al., 2005).

Most of the species present in urban areas are generalists, omnivorous and have high tolerance of human disturbance (Grimm et al., 2008; Lizée et al., 2011; Shochat et al., 2006). Successful urban species typically show plasticity in behaviours that help them to adjust to major environmental disturbances and exploit new niches. Yet, most urban species maintain a wary distance from humans, showing flight responses to human approach and close interactions (Carrete and Tella, 2011; Møller, 2008; Rodewald and Shustack, 2008). Studies on several urban-adapted mammals have shown that though they scavenge in human settlements, they prefer to build their dens away from humans, avoiding human proximity while giving birth to their offspring (Ross et al., 2010; Theuerkauf and Jedrzejewski, 2002; Ye et al., 2007). The dog, *Canis lupus familiaris* (Linnaeus 1758), has shared space with humans for centuries, being the first species to be domesticated by humans (Clutton-Brock, 1995). Though the domestic dog is mostly recognized as a pet, free-ranging dogs comprise almost 80% of the world's dog population (Boitani and Ciucci, 1995; Hughes and Macdonald, 2013), and are an integral part of the human environment in most developing countries (Vanak and Gompfer, 2009). They experience differing levels of human interactions, both positive and negative (Bhattacharjee et al., 2017b), and are largely dependent on human-generated waste for their sustenance (Sen Majumder et al., 2014). Free-ranging dogs are not under direct human supervision (Cafazzo et al., 2010; Sen Majumder et al., 2014; Vanak and Gompfer, 2009), but have adapted to living in close proximity with humans. They are also considered to be reservoirs of various zoonotic diseases including rabies, and therefore are a threat to both humans and wildlife (Butler et al., 2004; Fekadu, 1982). Moreover, they scatter garbage, defecate in open spaces and disturb people by their nocturnal barking. Hence, they are considered to be a nuisance by many humans, though they are often cared for by some. It is likely that their experiences of interactions with humans influence their behaviour to some extent, determining their perception of humans in general.

In India, free-ranging dogs have existed as a continuous population for centuries (Thapar, 1990). They have a ubiquitous presence ranging from remote villages to metropolitan areas. They are primarily scavengers, but are known to hunt in packs on the fringes of human habitations too (Kumar and Paliwal, 2015; Young et al., 2011). They live in stable social packs that show interesting cooperation–conflict dynamics, especially over pup rearing (Sen Majumder et al., 2014; Paul and Bhadra, 2017; Paul et al., 2014, 2015). Early-life mortality is very high in spite of extensive parental and alloparental care, with only 19% of pups reaching adulthood;

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Received 10 July 2017; Accepted 10 October 2017

63% of this mortality is human induced, including poisoning, beating and road accidents. In spite of this, the free-ranging dogs do not avoid human proximity during whelping, but often use spaces within human habitations as dens (Paul et al., 2016a; Sen Majumder et al., 2016). They show plasticity in their interactions with humans; pups readily follow human pointing gestures, but juveniles tend not to do so. Adults use reliability cues to adjust their responses to human pointing and are good at retrieving food from human artefacts like closed garbage bags (Bhattacharjee et al., 2017b). Humans are thus a source of food and shelter but are also responsible for the mortality of free-ranging dogs, and thus it is imperative for the dogs to assess the intentions of humans before interacting with them. It has been suggested that canines have a predisposition to attend to the actions of their social companions, and must learn to recognize humans as companions and understand the relationship through learning and experience (Reid, 2009). Moreover, social attachment with humans is considered to have been a key factor in dog domestication (Nagasawa et al., 2015). Here, we investigated the dog–human relationship in the context of food and social rewards in the urban environment, to better understand the ecology and behaviour of free-ranging dogs from the perspective of interspecific interactions.

A study by Feuerbacher and Wynne (2012) concluded there was no effect of a brief social reward on pet and shelter dogs as compared with a food reward, but contextual differences might play a determining role in the case of free-ranging dogs. Another study showed a tendency for pet dogs to prefer food to petting, but petting seemed to be important when it was compared with vocal praise (Feuerbacher and Wynne, 2014). Hence, without considering the effect of different environmental conditions and life experiences, direct comparison of outcomes from pet dogs with free-ranging dogs would not be valid. Field observations have allowed us to understand that free-ranging dogs receive both petting and ample food directly from humans only on rare occasions. However, being scavengers, they mostly forage for food in and around human settlements, and sometimes beg for food from humans by gazing at them, wagging their tails and, occasionally, holding out their tongues. We conducted field trials on free-ranging dogs to test the effect of food and social rewards on their tendency to make contact with unfamiliar humans. Our experiments comprised both one-off trials with brief exposure to social petting and long-term repeated trials for both kinds of reward. We provided dogs with a choice to obtain food from either a human hand or the ground. As free-ranging dogs are scavengers, and they also receive negative interactions from humans, we hypothesized that they would prefer to take food from the ground, rather than from the experimenter's hand. We expected that the immediate social reward would increase the dogs' tendency to take food from the hand. However, as pet dogs respond more to food than to petting, we expected the free-ranging dogs to show an increased tendency to feed from the experimenter's hand when provided with food in the long-term trials rather than social rewards.

MATERIALS AND METHODS

Subjects and study area

We tested a total of 103 adult free-ranging dogs located randomly in different urban areas: Mohanpur (22°56'49"N and 88°32'4"E), Kalyani (22°58'30"N, 88°26'04"E) and Kolkata (22°57'26"N, 88°36'39"E), West Bengal, India. We confirmed that all the individuals were physically fit and not injured during the test. To avoid any influence of other dogs, we tried to locate solitary individuals for the test. As dogs often tend to forage alone (Majumder et al., 2014b),

this was not very difficult. When an individual from a group was tested, other members were lured away from the focal dog. The sex and age class (adults/juvenile) of the focal individual was recorded, but the exact age could not be determined. All the dogs were strangers to the experimenter. All individuals were photographed for record and tracking purpose. The individuals were tracked for the long-term experiments using their location and morphological features like coat colour, patch patterns and any other distinguishing features on the body.

Experimental procedure

One-off test

We used 30 random adult dogs to test their tendency to approach unfamiliar humans for food. A single piece of raw chicken weighing approximately 10–15 g was used as the food reward. In trial 1, the experimenter placed a food reward in the palm of his hand (left or right hand chosen randomly) and held it open close to the ground, at a height of 5–10 cm. At the same time, the experimenter placed a similar piece of raw chicken on the ground in front of him, such that there was a distance of 0.6 m between the two reward options. The set-up was designed such that the two reward options were equally accessible to the dog (Fig. S1, Movie 1). The experimenter tried to attract the attention of an individual dog using sounds that are typically used to call out to dogs on streets in India (Movie 2) for 1–2 s, from an approximate distance of 1.2 m. As these dogs were not on leash, we tried to ensure that the distance remained roughly the same before recording the trials. The response of the dog was video recorded for 1 min or until an individual made a choice, whichever was earlier. Obtaining a reward from either of the locations terminated the trial. Thus, an individual could get only one piece of chicken in a trial. The experimenter kept gazing at the dog throughout the trial, but eye contact was established only when an individual reciprocated gazing. The same person carried out all the trials. After completion of trial 1, the experimenter provided the dog with a social reward by petting it 3 times on its head. After an interval of 5–10 s, trial 2 was run, where the individuals again had to make a choice from the same set-up as in trial 1.

The control trials were exactly the same as the test trials, but the experimenter did not provide any social reward in between trials 1 and 2. A separate set of 30 adult dogs were tested in this condition.

Long-term test

A total of 43 adult dogs, different from those used in the one-off test and control trials, were randomly selected for a long-term experiment in order to investigate the effect of learning in the context of food and social rewards. From this set of 43 individuals, two subsets were randomly generated: 21 individuals for food rewards and 22 individuals for social rewards. Each dog was tested a total of 6 times, at increasing intervals of 1, 2, 3, 4 and 5 days. Thus, for every dog, the experiment commenced on day 0, and was conducted on days 1, 3, 6, 10 and 15, respectively. Unlike the one-off test and control conditions, in this case, only trial 1 was run, keeping the protocol constant. Additional food (one piece of chicken) or social (petting thrice on the head) rewards were provided by the experimenter, 1 min before the trial, to the respective subsets of dogs except on day 0. The experimenter stood in a neutral posture and provided the additional piece of food reward by throwing it on the ground. Thus, differential postures and methods were used while testing and providing additional food rewards in order to eliminate any bias towards the food options. On day 0, no additional food or social reward was provided, such that this represented the response of the naive dogs to the experimenter.

Data analysis

All the videos were coded by D.B., and the data were used for further analysis. We used Shapiro–Wilk tests to check for normality of our data and found that they were not normally distributed; thus, we performed non-parametric tests.

We considered all the ‘naive’ responses – trial 1 of the one-off test and control conditions and the day 0 responses of long-term observations – in order to investigate the population-level preference of dogs by characterizing their choice between food offered from the hand directly and food placed on the ground. We compared the number of dogs that obtained food from the ground and the human hand using goodness of fit chi-squared tests. We defined latency as the time between catching the attention of an individual dog and its approach to either of the options provided. We compared latencies of the dogs that obtained food from the ground and from the hand using Mann–Whitney *U*-tests. We identified the sex of the dogs and compared the response of the two sexes in obtaining food rewards using contingency chi-squared test. We calculated all possible combinations (hand–hand, ground–hand, ground–ground and hand–ground) of obtaining the food reward by dogs between trials 1 and 2 of both test and control conditions. Hand–hand and ground–ground situations were considered as ‘no change’ and hand–ground and ground–hand situations as ‘change’. We then compared change and no change categories for both test and control trials by using goodness of fit chi-squared tests. We compared latencies of dogs between trials 1 and 2 for both the test and control conditions using Wilcoxon paired-sample tests.

We built a socialization index based on the vigour of tail wagging and gazing at different food reward options by the dogs (Table 1). Tail wagging by free-ranging dogs establishes an affirmative association with humans and is indicative of a positive social bond. Free-ranging dogs exhibit proximity-seeking behaviour by showing frequent tail wagging along with gazing when faced with an unfamiliar solvable task (Bhattacharjee et al., 2017a). Thus, tail wagging in this circumstance was considered to be an affirmative behaviour. Gazing or alternation of gaze indicates a free-ranging dog’s hesitant nature to approach any of the food options (Bhattacharjee et al., 2017b). Thus, we assumed that a slower response and prolonged gazing could be attributed to the dog’s hesitant nature, familiarizing itself with the set-up or attentional bias. Scores were assigned in such a way that an individual could have a maximum index value of 8 by showing rapid tail wagging and no gazing at all.

We compared the index values of individuals across the two trials for both test and control conditions using Wilcoxon paired-sample tests. Generalized linear mixed models (GLMM) with binomial distributions were used to check any effect of time interval, latency

and socialization index values over the dogs’ preference for obtaining food reward from either the hand or ground in long-term experiments.

Separate models (GLMM) were built for the two different conditions where additional food and social rewards were provided. Identity of the individuals was included as a random effect on the intercept. We used AIC values for comparison in order to get the best-fitting models. We determined the consistency of individuals obtaining the food reward from the hand and ground at 100% and 80% levels for both the long-term experiments. Similarly, overall inconsistency was calculated where dogs changed their preference on every alternate day interval.

A second coder naive to the purpose of the study coded 20% of the data to check inter-rater reliability. It was perfect food preference (Cohen’s kappa=1.00) and socialization index building (Cohen’s kappa=1.00) and almost perfect for latency (Cohen’s kappa=0.95). The alpha level was 0.05 throughout the analysis. GLMMs were performed using lme4 package of R Studio (R Development Core Team, 2015). Along with R, other statistical analyses were performed using Statistix version 1.11.0.0.

RESULTS

Attachment of dogs to humans

Considering the ‘naive’ responses of all 103 individuals, 37% obtained the food reward from the human hand and 63% from the ground, thereby showing a bias against making physical contact with the experimenter (Fig. 1, goodness of fit; $\chi^2=7.078$, d.f.=1, $P=0.008$). However, we did not see any difference in latency to approach between the responders that showed different choices (Mann–Whitney *U*-test; $U=1301.00$, d.f.1=38, d.f.2=65, $P=0.65$), which suggests that the final choice did not influence the time taken to reach a decision to respond. The two sexes were comparable in their preference to obtain food from either the hand or the ground (contingency χ^2 ; $\chi^2=1.573$, d.f.=1, $P=0.21$).

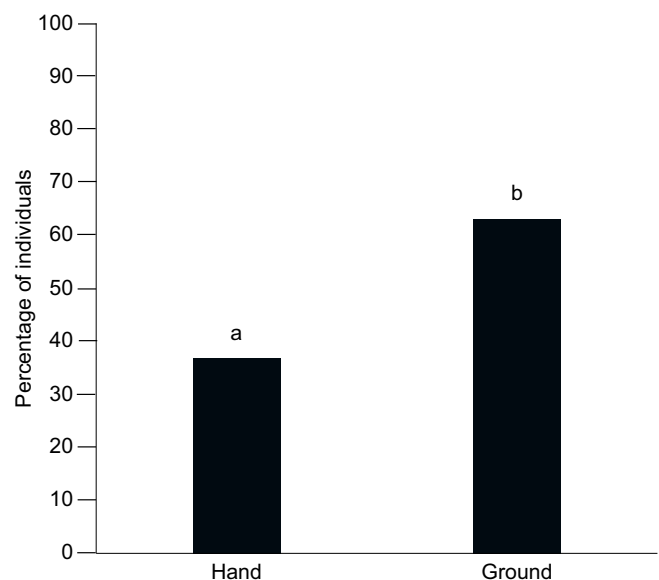


Fig. 1. Response to unfamiliar humans. Bar graph showing the percentage of individual dogs that obtained a food reward from a human hand or the ground out of all naive responses. Dogs ($N=103$) showed a significantly higher tendency to obtain the reward from the ground (goodness of fit; $\chi^2=7.078$, $P=0.008$). Different letters indicate a significant difference between the categories.

Table 1. Socialization index incorporating the behaviours shown by dogs and corresponding scores

Tail wagging		Gazing	
Type	Score	Type	Score
Rapid (in combination with back movement)	4	No	4
Fast (without back movement)	3	At hand food	3
Slow	2	At both hand and ground food	2
No	1	At ground food	1

The socialization index was built based on tail wagging and gazing behaviour. Definitions of different types of tail wagging and gazing behaviours and their corresponding scores within a range of 1 to 4 are provided.

Effect of immediate social reward/petting

We found that in the one-off test, 73% and 83% of the individuals showed 'no change' in their response in trial 2 for the test and control conditions, respectively. For both the conditions, the proportion of 'no change' responses was significantly higher than the proportion of 'change' responses (test-goodness of fit; $\chi^2=6.533$, d.f.=1, $P=0.01$; control- $\chi^2=13.333$, d.f.=1, $P<0.001$), suggesting no effect of immediate social reward (Fig. 2). Interestingly, we found a faster approach by dogs to the set-up in trial 2 for the test condition; thus, the latency significantly decreased when social reward was provided (Wilcoxon paired-sample test; $T=86.00$, $N=30$, $P=0.004$), but it remained unchanged in the control condition, when no social reward was provided (Fig. 3, Wilcoxon paired-sample test; $T=166.500$, $N=30$, $P=0.427$). As separate sets of individuals were present for the test and control conditions, we compared the latency of trials 1 and 2 between test and control conditions. We found no difference for trial 1 latencies of the two conditions (Mann–Whitney U -test; $U=480.00$, d.f.=30, d.f.=30, $P=0.66$), but noticed a significant difference between the trial 2 latencies (Mann–Whitney U -test; $U=584.500$, d.f.=30, d.f.=30, $P=0.04$). These results suggest that the dogs might be prone to showing a stronger response to humans when they receive positive social interactions. However, we did not find any difference in socialization index values between trials 1 and 2 for both test (Wilcoxon paired-sample test; $T=73.500$, $N=30$, $P=0.14$) and control conditions (Wilcoxon paired-sample test; $T=111.500$, $N=30$, $P=0.20$).

Effect of long-term social and additional food rewards

Based on AIC values, the best-fitting model depicted socialization index to be the only significant predictor of the dogs' preference for

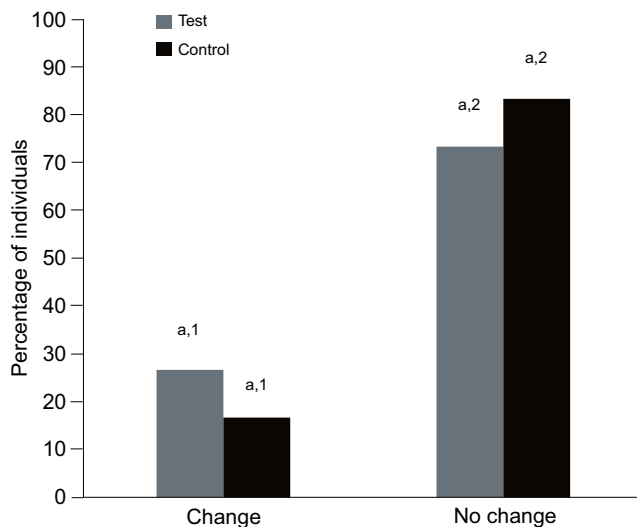


Fig. 2. Effect of immediate social reward. Bar graph illustrating the percentage of individuals showing 'change' and 'no change' responses for the food reward preference in the second trial under test and control conditions. 'No change' indicates the same preference of obtaining food in trial 1 and 2 (hand–hand, ground–ground). 'Change' indicates a change or switch in preference from trial 1 to trial 2 (hand–ground, ground–hand). Responses in the test (social reward) condition and the control (no social reward) condition are shown. Different letters indicate a significant difference within categories (within change and within no change). Different numbers indicate a significant difference between categories. The proportion showing no change was significantly higher than the proportion showing change ($N=60$; test-goodness of fit; $\chi^2=6.533$, d.f.=1, $P=0.01$; control- $\chi^2=13.333$, d.f.=1, $P<0.001$).

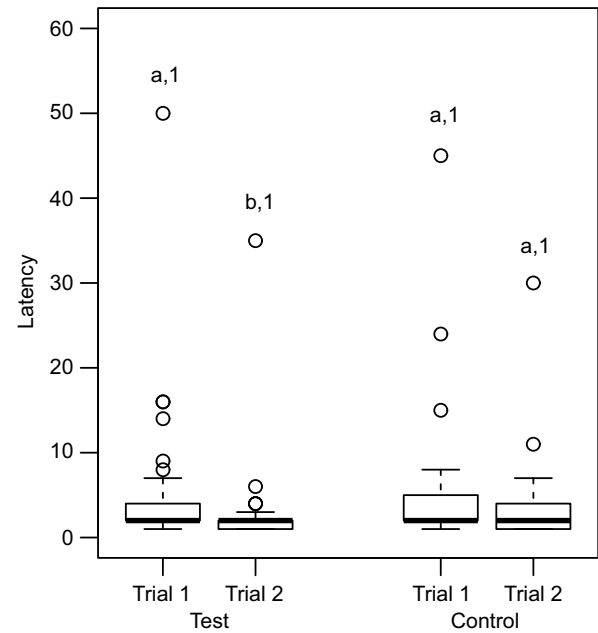


Fig. 3. Latency to approach the experimental set-up. Dogs showed a significant difference in latency between trials 1 and 2 for the test (social reward) condition (Wilcoxon paired-sample test; $T=86.00$, $N=30$, $P=0.004$). Latency remained comparable between trials 1 and 2 in the control (no social reward) condition (Wilcoxon paired-sample test; $T=166.500$, $N=30$, $P=0.427$). Boxes represent interquartile range, horizontal bars within boxes indicate median values, and whiskers represent the upper range of the data. Different letters indicate a significant difference within categories. Different numbers indicate a significant difference between categories.

obtaining food in the long-term experiment with additional food reward (Fig. 4; Table S1). However, we found socialization index, latency and time interval to be significant predictors of the response in the long-term experiment with social rewards (Fig. 5; Table S2). In the long-term additional food reward experiment, 11 out of 21 individuals (52%) were 100% consistent for obtaining food reward

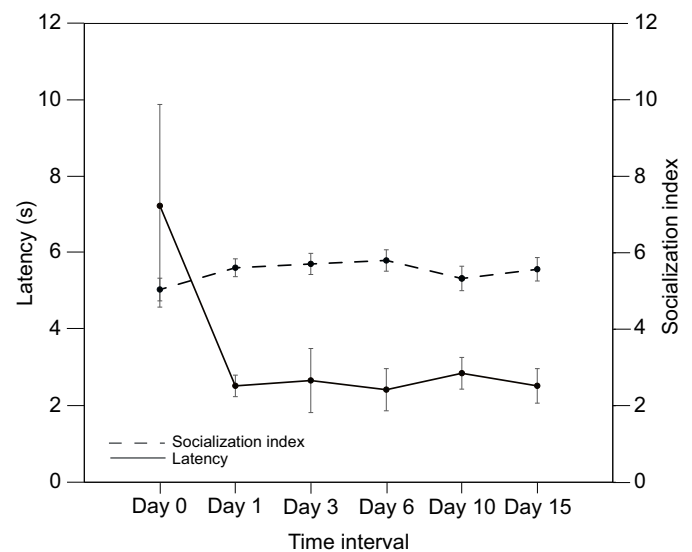


Fig. 4. Average latency and socialization index values at different intervals for the long-term additional food reward condition. Data are means \pm s.e. The solid line indicates latency and the dashed line indicates socialization index.

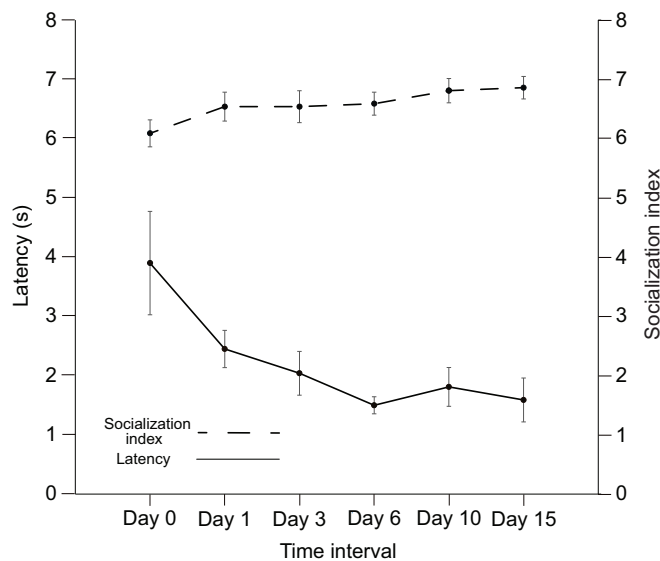


Fig. 5. Average latency and socialization index values at different intervals for the long-term social reward condition. Data are means \pm s.e. The solid line indicates latency and the dashed line indicates socialization index.

from the ground, whereas only a single individual consistently obtained food from the hand (Fig. 6, goodness of fit; $\chi^2=8.333$, d.f.=1, $P=0.004$). In the long-term social reward experiment, 3 out of 22 (14%) and 8 out of 22 (36%) individuals showed 100% consistency for obtaining food from the ground and hand, respectively (Fig. 7, goodness of fit; $\chi^2=2.273$, d.f.=1, $P=0.13$). We found a difference in the 100% consistency levels for obtaining food from the hand and ground between social and additional food reward conditions (contingency chi-square; $\chi^2=9.991$, d.f.=1, $P=0.002$). At 80% consistency level, 3 out of 21 (14%) and 1 out of 21 (5%) individuals obtained the food reward from the hand and

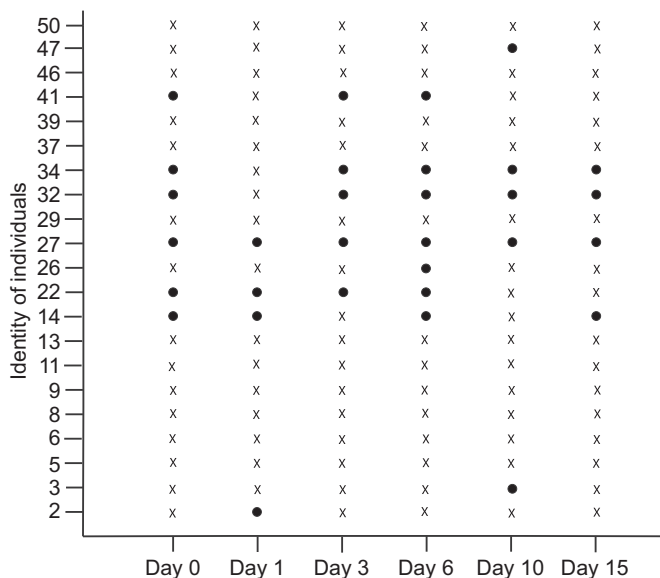


Fig. 6. Identity of individuals and their preference for obtaining the reward at specific intervals for the long-term additional food reward condition. The circles indicate that food was obtained from the hand and the crosses indicate that food was obtained from the ground. Day 0 responses are naive as dogs had had no previous exposure to the additional food reward.

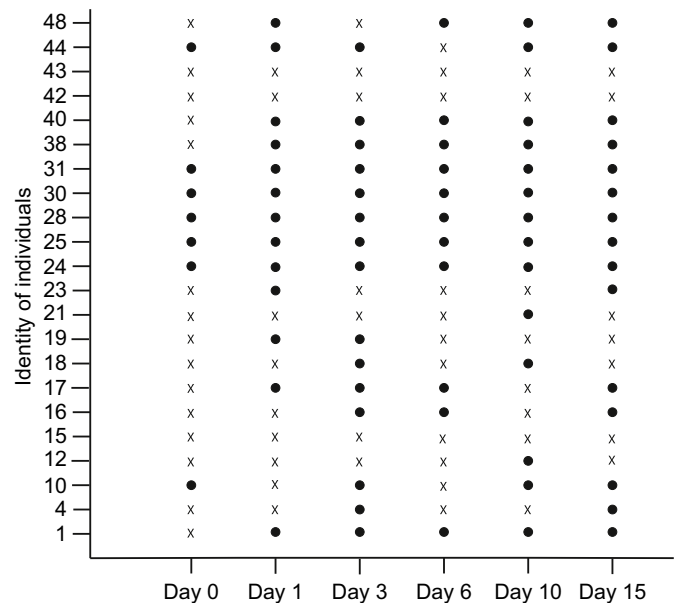


Fig. 7. Identity of individuals and their preference for obtaining the reward at specific intervals for the long-term social reward condition. The circles indicate that food was obtained from the hand and the crosses indicate that food was obtained from the ground. Day 0 responses are naive as dogs had had no previous exposure to the social reward.

ground (goodness of fit; $\chi^2=1.000$, d.f.=1, $P=0.32$), respectively, for the additional food reward condition, whereas none of the individuals from the social reward condition showed 80% consistency. One out of 21 individuals for the additional food reward and 1 out of 22 individuals for the social reward condition changed their responses on every alternate day of the experiment, thereby showing inconsistency.

DISCUSSION

Free-ranging dogs demonstrated a bias against making physical contact with unfamiliar humans, as suggested by the higher proportion of individuals opting to take the food from the ground, validating our hypothesis. In the one-off test, dogs elicited a significantly faster response (reduced latency) or an increased tendency to approach the set-up when the social reward was provided. However, contrary to our expectations, a single positive feedback in terms of social reward did not prove to be substantial in establishing trust of the unfamiliar human. Moreover, it did not translate into an increased tendency to interact with the experimenter as there was no change in the socialization index between consecutive trials after the social reward was provided. The one-off experiments thereby reinforce the idea that free-ranging dogs are generally wary of humans (Bhattacharjee et al., 2017b), and prefer not to make physical contact with unfamiliar humans, even after receiving brief positive reinforcement through food or social rewards.

The long-term experiments provided an interesting insight into the free-ranging dogs' relationship with humans, which was very different from our hypothesis based on the results obtained with pet dogs in the past (Feuerbacher and Wynne, 2012). Long-term provisioning of an additional food reward increased the socialization index values of dogs that obtained the food reward from the human hand. However, there was no significant reduction in the latency to respond, which suggests that the dogs were hesitant to make direct contact with humans, despite increasing familiarity and

positive reinforcement with the additional food reward. The most striking observation was the change in the dogs' response to the experimenter in the presence of the long-term social reward. Dogs exposed to the social reward showed reduced latency (thus increased interest) to approach the experimenter and an increase in the socialization index. Moreover, the dogs' preference to feed from the human hand increased with increased exposure to the social reward. The high degree of consistency shown by the dogs in obtaining food from the ground in the additional food reward condition further validates their predisposition to avoid physical contact with unfamiliar humans. In contrast, a higher number of dogs showed 100% consistency in preferentially taking food from the human hand in the social reward condition. Our results with the free-ranging dogs could potentially be the outcome of several underlying factors such as the level of previous interactions with humans, scavenging and begging abilities, dominant nature of an individual, etc. Companion dogs receive a substantial amount of social contact from their owners, unlike the free-ranging dogs, and thus a differential level of human socialization also exists. To summarize, long-term social reward, but not food reward, impacted dogs' tendency to make physical contact with humans, which suggests that social reward is more effective in building trust between free-ranging dogs and unfamiliar humans than food rewards.

A recent study concluded that domestication has been a key factor contributing to dogs' capacity to engage in visual and physical contact with humans (Nagasawa et al., 2015). It has been suggested that short-term sensory interactions between pet dogs and their owners influence hormone levels (e.g. oxytocin) and heart rate (Handlin et al., 2011). Rising levels of oxytocin in dogs help to maintain their social orientation, affiliation and gazing toward their owners (Nagasawa et al., 2015; Romero et al., 2014), and gazing towards dogs increases the oxytocin levels in their owners, which in turn induces a rise in oxytocin in the dogs, thus strengthening the dog–human bonding (Nagasawa et al., 2015). Though free-ranging dogs tend to avoid direct human contact, studies have shown that they gaze and even seek help from strangers when faced with an unfamiliar task (Bhattacharjee et al., 2017a). Free-ranging dogs are also known to regularly beg from humans, using the gazing behaviour (Bhadra and Bhadra, 2014). They often experience negative interactions with humans, and their tendency to avoid direct physical contact with unfamiliar humans could be a possible outcome of cumulative negative experiences. In our experiment with the long-term additional reward conditions, the dogs preferred to avoid contact when the experimenter provided an additional food reward. However, long-term social reward increased the dogs' tendency to make physical contact with the experimenter. In their day-to-day lives, the free-ranging dogs routinely encounter unfamiliar humans, and the ability to assess human intentions could be highly adaptive under such circumstances. They are often lured with food and then beaten up or even poisoned by people (Paul et al., 2016b) and, hence, relying on strangers who offer food might have negative consequences for dogs. However, people who show affection to the dogs are less likely to harm them, and relying on such humans might indeed be advantageous.

In an earlier study, we observed pups to readily follow human pointing, while juveniles and adults fail to do so. Interestingly, adults adjust their reliability on the experimenter based on immediate experience, choosing to follow pointing on positive reinforcement and refusing to follow pointing on negative reinforcement (Bhattacharjee et al., 2017b). Thus, the free-ranging dogs show considerable plasticity in their tendency to follow human pointing, learning from experience through their development. The

ability to follow human pointing is considered to be an important socio-cognitive ability in dogs, and has been suggested to be closely associated with their domestication (Hare and Tomasello, 2005; Miklósi et al., 2004; Miklósi et al., 1998; Paul et al., 2016b; Soproni et al., 2001). The free-ranging dogs in India live very closely with humans, in every possible human habitation, and are dependent on humans for their sustenance, either directly or indirectly (Sen Majumder et al., 2014, 2016; Vanak and Gompfer, 2009). In contrast to other urban-adapted animals, the free-ranging dogs have been observed to preferentially form dens close to humans, often within human homes (Sen Majumder et al., 2016). They interact with familiar as well as unfamiliar humans on a regular basis and receive both positive and negative interactions from them. During the early stages of domestication, ancestors of the present-day dogs would have been faced with a similar situation. Human communities would have acted as a lucrative source of nutrition, but the adventurous individuals that ventured too close could have been easy prey for the humans. Someone who threw a bone to a dog could have turned into a hunter in no time, but a human who put out a friendly hand to pet a dog would have been less likely to attack it. The oxytocin feedback that is known to help establish bonding between dogs and their owners could have been influential in this trust-building phase of the relationship between the two species. We speculate that the tendency of dogs to also rely on positive social interactions for trust building with unfamiliar humans could have acted as an important behavioural paradigm in the evolution of the dog–human relationship.

Acknowledgements

The authors thank Mr Susnata Karmakar, IISER Kolkata, for lending us his vehicle for use during the field experiments.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.B., A.B.; Methodology: D.B., S.S., J.D., A.B.; Software: A.B.; Validation: A.B.; Formal analysis: D.B., J.D.; Investigation: D.B., S.S., J.D.; Resources: A.B.; Writing - original draft: D.B., J.D.; Writing - review & editing: D.B., A.B.; Supervision: A.B.; Project administration: A.B.; Funding acquisition: A.B.

Funding

This research was supported by the Department of Science and Technology, Ministry of Science and Technology (INSPIRE fellowship to D.B.; INSPIRE scholarship to J.D.).

Data availability

Data are available from the Dryad Digital Repository (Bhattacharjee et al., 2017): <https://doi.org/10.5061/dryad.p63q0>.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.166371.supplemental>

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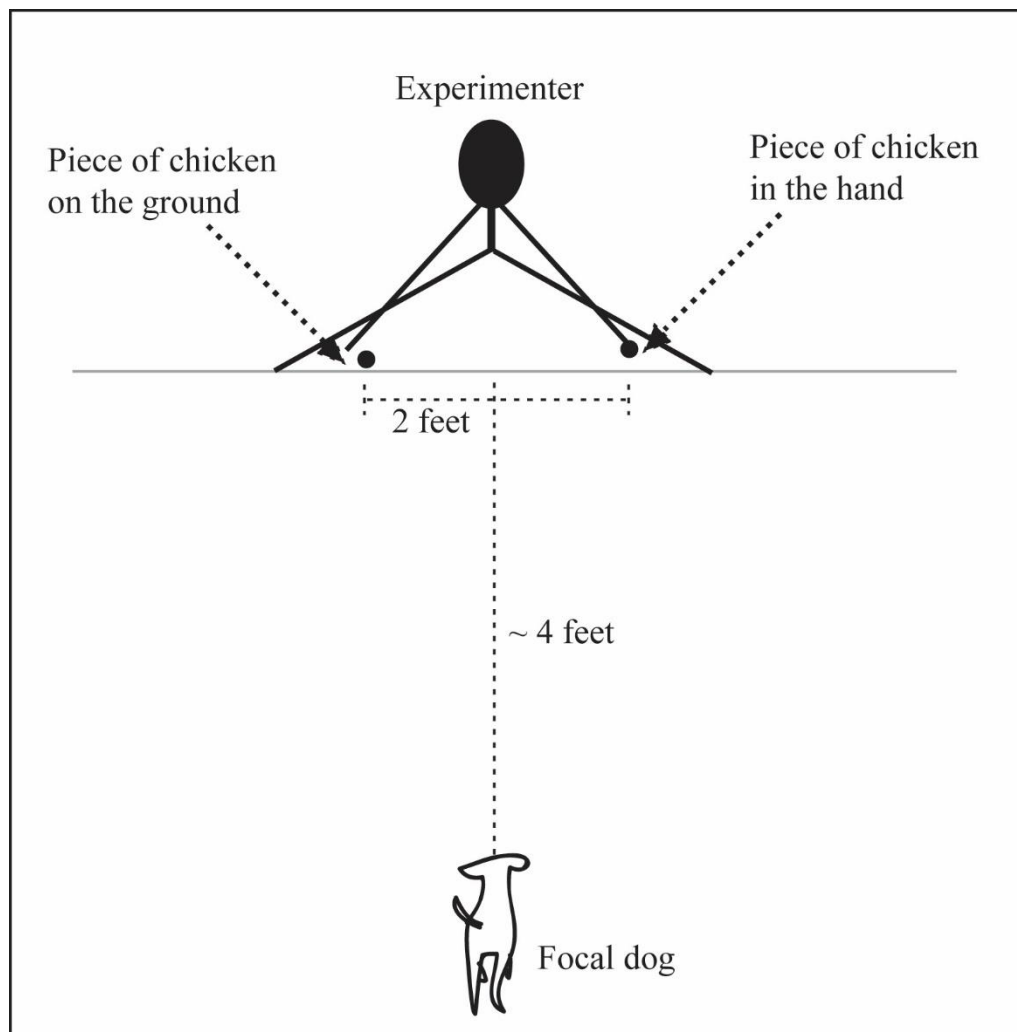


Fig. S1. Schematic representation of the experimental set-up.



Movie 1. Protocol used for the one-off test.



Movie 2. Calling dogs on streets in India.

Table S1. Effect of parameters (time interval, socialization index and latency) on long-term feeding (ground or hand) preference for additional food reward condition using Generalized Linear Mixed Model

Predictors – Day interval (day), Socialization index (bi), latency (latency)
Response – Feeding from hand / ground (feed)
Random effect – Identity of individuals (ind)

Model 1:																																																		
<pre>> lrfit01 <- glmer(feed ~ day+bi+latency + (1 ind) , data=food,</pre>																																																		
<pre>+ family = binomial, glmerControl(optimizer = "bobyqa"))</pre>																																																		
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [
glmerMod]																																																		
Family: binomial (logit)																																																		
Formula: feed ~ day + bi + latency + (1 ind)																																																		
Data: food																																																		
Control: glmerControl(optimizer = "bobyqa")																																																		
<table><tr><td>AIC</td><td>BIC</td><td>logLik</td><td>deviance</td><td>df.resid</td></tr><tr><td>90.2</td><td>115.7</td><td>-36.1</td><td>72.2</td><td>117</td></tr></table>						AIC	BIC	logLik	deviance	df.resid	90.2	115.7	-36.1	72.2	117																																			
AIC	BIC	logLik	deviance	df.resid																																														
90.2	115.7	-36.1	72.2	117																																														
Scaled residuals:																																																		
<table><tr><td>Min</td><td>1Q</td><td>Median</td><td>3Q</td><td>Max</td></tr><tr><td>-1.6919</td><td>-0.2419</td><td>-0.1150</td><td>-0.0133</td><td>3.2908</td></tr></table>						Min	1Q	Median	3Q	Max	-1.6919	-0.2419	-0.1150	-0.0133	3.2908																																			
Min	1Q	Median	3Q	Max																																														
-1.6919	-0.2419	-0.1150	-0.0133	3.2908																																														
Random effects:																																																		
<table><tr><td>Groups</td><td>Name</td><td>Variance</td><td>Std.Dev.</td></tr><tr><td>ind</td><td>(Intercept)</td><td>1.816</td><td>1.348</td></tr></table>						Groups	Name	Variance	Std.Dev.	ind	(Intercept)	1.816	1.348																																					
Groups	Name	Variance	Std.Dev.																																															
ind	(Intercept)	1.816	1.348																																															
Number of obs: 126, groups: ind, 21																																																		
Fixed effects:																																																		
<table><tr><td></td><td>Estimate</td><td>Std. Error</td><td>z value</td><td>Pr(> z)</td></tr><tr><td>(Intercept)</td><td>-13.10637</td><td>2.96509</td><td>-4.420</td><td>9.86e-06 ***</td></tr><tr><td>day1</td><td>-1.91762</td><td>1.24256</td><td>-1.543</td><td>0.1228</td></tr><tr><td>day3</td><td>-1.63570</td><td>1.18927</td><td>-1.375</td><td>0.1690</td></tr><tr><td>day6</td><td>-0.90371</td><td>1.18678</td><td>-0.761</td><td>0.4464</td></tr><tr><td>day10</td><td>-1.07413</td><td>1.23084</td><td>-0.873</td><td>0.3828</td></tr><tr><td>day15</td><td>-2.70258</td><td>1.35941</td><td>-1.988</td><td>0.0468 *</td></tr><tr><td>bi</td><td>2.11886</td><td>0.47461</td><td>4.464</td><td>8.03e-06 ***</td></tr><tr><td>latency</td><td>0.07831</td><td>0.06892</td><td>1.136</td><td>0.2558</td></tr></table>							Estimate	Std. Error	z value	Pr(> z)	(Intercept)	-13.10637	2.96509	-4.420	9.86e-06 ***	day1	-1.91762	1.24256	-1.543	0.1228	day3	-1.63570	1.18927	-1.375	0.1690	day6	-0.90371	1.18678	-0.761	0.4464	day10	-1.07413	1.23084	-0.873	0.3828	day15	-2.70258	1.35941	-1.988	0.0468 *	bi	2.11886	0.47461	4.464	8.03e-06 ***	latency	0.07831	0.06892	1.136	0.2558
	Estimate	Std. Error	z value	Pr(> z)																																														
(Intercept)	-13.10637	2.96509	-4.420	9.86e-06 ***																																														
day1	-1.91762	1.24256	-1.543	0.1228																																														
day3	-1.63570	1.18927	-1.375	0.1690																																														
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bi	2.11886	0.47461	4.464	8.03e-06 ***																																														
latency	0.07831	0.06892	1.136	0.2558																																														

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1																																																		
Correlation of Fixed Effects:																																																		
<table><tr><td></td><td>(Intr)</td><td>day1</td><td>day3</td><td>day6</td><td>day10</td><td>day15</td><td>bi</td></tr><tr><td>day1</td><td></td><td>0.024</td><td></td><td></td><td></td><td></td><td></td></tr><tr><td>day3</td><td></td><td>0.017</td><td>0.540</td><td></td><td></td><td></td><td></td></tr></table>							(Intr)	day1	day3	day6	day10	day15	bi	day1		0.024						day3		0.017	0.540																									
	(Intr)	day1	day3	day6	day10	day15	bi																																											
day1		0.024																																																
day3		0.017	0.540																																															

day6	-0.029	0.525	0.558				
day10	-0.045	0.496	0.521	0.518			
day15	0.222	0.539	0.551	0.518	0.488		
bi	-0.943	-0.235	-0.244	-0.209	-0.166	-0.424	
latency	-0.492	0.138	0.170	0.195	0.150	0.064	0.365
Model 2:							
> lrfmt02 <- glmer(feed ~ bi+latency + (1 ind) , data=food,							
+ family = binomial, glmerControl(optimizer = "bobyqa"))							
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [
glmerMod]							
Family: binomial (logit)							
Formula: feed ~ bi + latency + (1 ind)							
Data: food							
Control: glmerControl(optimizer = "bobyqa")							
AIC BIC logLik deviance df.resid							
85.7 97.0 -38.8 77.7 122							
Scaled residuals:							
Min 1Q Median 3Q Max							
-1.9369 -0.2782 -0.1512 -0.0257 3.5909							
Random effects:							
Groups Name Variance Std.Dev.							
ind (Intercept) 1.501 1.225							
Number of obs: 126, groups: ind, 21							
Fixed effects:							
Estimate Std. Error z value Pr(> z)							
(Intercept) -13.06853 2.70265 -4.835 1.33e-06 ***							
bi 1.89215 0.41092 4.605 4.13e-06 ***							
latency 0.09984 0.06024 1.657 0.0974 .							

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1							
Correlation of Fixed Effects:							

(Intr) bi
bi -0.981
latency -0.500 0.445
Model 3:
> lrfit03 <- glmer(feed ~ latency*day + (1 ind) , data=food,
+ family = binomial, glmerControl(optimizer = "bobyqa"))
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [
glmerMod]
Family: binomial (logit)
Formula: feed ~ latency * day + (1 ind)
Data: food
Control: glmerControl(optimizer = "bobyqa")
AIC BIC logLik deviance df.resid
121.2 158.1 -47.6 95.2 113
Scaled residuals:
Min 1Q Median 3Q Max
-1.57079 -0.21714 -0.11576 -0.01109 3.15089
Random effects:
Groups Name Variance Std.Dev.
ind (Intercept) 10.64 3.262
Number of obs: 126, groups: ind, 21
Fixed effects:
Estimate Std. Error z value Pr(> z)
(Intercept) -2.18766 1.53964 -1.421 0.155
latency -0.03937 0.14875 -0.265 0.791
day1 -2.84978 2.09151 -1.363 0.173
day3 -0.29373 2.24816 -0.131 0.896
day6 0.40958 1.54596 0.265 0.791
day10 1.27589 1.98735 0.642 0.521
day15 -1.42551 1.84723 -0.772 0.440
latency:day1 0.68205 0.67915 1.004 0.315
latency:day3 -0.26339 1.23350 -0.214 0.831
latency:day6 -0.01155 0.42843 -0.027 0.978
latency:day10 -0.76239 0.62968 -1.211 0.226

latency:day15	0.05456	0.62812	0.087	0.931					
Correlation of Fixed Effects:									
(Intr)	latncy	day1	day3	day6	day10	day15	ltnc:1	ltnc:	
3	ltnc:6								
latency	-0.503								
day1	-0.183	0.331							
day3	-0.200	0.296	0.341						
day6	-0.467	0.474	0.325	0.305					
day10	-0.379	0.381	0.282	0.224	0.385				
day15	-0.294	0.386	0.381	0.296	0.392	0.341			
latency:dy1	-0.059	-0.203	-0.836	-0.198	-0.092	-0.116	-0.192		
latency:dy3	-0.056	-0.092	-0.157	-0.846	-0.052	-0.024	-0.080	0.157	
latency:dy6	0.117	-0.333	-0.153	-0.144	-0.700	-0.166	-0.184	0.107	0.07
latency:dy10	0.149	-0.252	-0.093	-0.047	-0.147	-0.802	-0.148	0.074	-0.00
latency:dy15	0.051	-0.235	-0.166	-0.087	-0.134	-0.162	-0.764	0.141	0.03
2	0.135								
ltnc:10									
latency									
day1									
day3									
day6									
day10									
day15									
latency:dy1									
latency:dy3									
latency:dy6									
latency:dy10									
latency:dy15	0.149								
> anova(lrfit100, lrfit101)									
Data: food									
Models:									
lrfit101: feed ~ bi + latency + (1 ind)									
lrfit100: feed ~ day + bi + latency + (1 ind)									
	Df	AIC	BIC	logLik	deviance	Chisq	Chi	Df	Pr(>Chisq)
lrfit101	4	85.683	97.029	-38.842	77.683				
lrfit100	9	90.159	115.685	-36.079	72.159	5.5247		5	0.3552

Table S2. Effect of parameters (time interval, socialization index and latency) on long-term feeding (ground or hand) preference for social reward condition using Generalized Linear Mixed Model

Predictors – Day interval (day), Socialization index (bi), latency (latency)				
Response – Feeding from hand / ground (feed)				
Random effect – Identity of individuals (ind)				
Model 1:				
<pre>> lrfit01 <- glmer(feed ~ day+bi+latency + (1 ind) , data=social,</pre>				
<pre>+ family = binomial, glmerControl(optimizer = "bobyqa"))</pre>				
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [
glmerMod]				
Family: binomial (logit)				
Formula: feed ~ day + bi + latency + (1 ind)				
Data: social				
Control: glmerControl(optimizer = "bobyqa")				
AIC BIC logLik deviance df.resid				
145.0 170.9 -63.5 127.0 123				
Scaled residuals:				
Min 1Q Median 3Q Max				
-2.2262 -0.3800 0.1067 0.3836 2.5167				
Random effects:				
Groups Name Variance Std.Dev.				
ind (Intercept) 6.846 2.616				
Number of obs: 132, groups: ind, 22				
Fixed effects:				
Estimate Std. Error z value Pr(> z)				
(Intercept) -7.8184 2.7953 -2.797 0.00516 **				
day1 2.5147 1.0566 2.380 0.01731 *				
day3 3.5102 1.1463 3.062 0.00220 **				
day6 1.8797 1.0410 1.806 0.07097 .				
day10 2.9811 1.1348 2.627 0.00862 **				
day15 3.3333 1.1776 2.831 0.00465 **				
bi 0.8148 0.3714 2.194 0.02827 *				

latency	0.3027	0.1401	2.161	0.03067	*

Signif. codes:	0 '***'	0.001 '**'	0.01 '*'	0.05 '.'	0.1 ' ' 1
Correlation of Fixed Effects:					
	(Intr)	day1	day3	day6	day10 day15 bi
day1	-0.297				
day3	-0.372	0.640			
day6	-0.234	0.618	0.623		
day10	-0.284	0.641	0.667	0.637	
day15	-0.263	0.633	0.661	0.632	0.667
bi	-0.917	0.045	0.118	-0.036	0.018 -0.005
latency	-0.563	0.376	0.447	0.413	0.433 0.440 0.367
Model 2:					
<pre>> lrfmt02 <- glmer(feed ~ bi+day + (1 ind) , data=social, + family = binomial, glmerControl(optimizer = "bobyqa"))</pre>					
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [
glmerMod]					
Family: binomial (logit)					
Formula: feed ~ bi + day + (1 ind)					
Data: social					
Control: glmerControl(optimizer = "bobyqa")					
AIC	BIC	logLik	deviance	df.resid	
147.4	170.5	-65.7	131.4	124	
Scaled residuals:					
Min	1Q	Median	3Q	Max	
-2.3493	-0.4183	0.1405	0.4207	2.3485	
Random effects:					
Groups	Name	Variance	Std.Dev.		
ind	(Intercept)	5.014	2.239		
Number of obs: 132, groups: ind, 22					
Fixed effects:					
	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-5.2176	2.2710	-2.297	0.02159	*
bi	0.6045	0.3349	1.805	0.07105	.

day1	1.9627	0.9485	2.069	0.03853	*	
day3	2.7672	1.0112	2.736	0.00621	**	
day6	1.1664	0.9201	1.268	0.20492		
day10	2.2434	1.0029	2.237	0.02529	*	
day15	2.5420	1.0292	2.470	0.01351	*	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1						
Correlation of Fixed Effects:						
	(Intr)	bi	day1	day3	day6	day10
bi	-0.929					
day1	-0.164	-0.070				
day3	-0.216	-0.011	0.600			
day6	-0.075	-0.160	0.583	0.565		
day10	-0.108	-0.126	0.602	0.605	0.582	
day15	-0.084	-0.149	0.599	0.604	0.578	0.612
Model 3:						
<pre>> lrfmt03 <- glmer(feed ~ day+latency + (1 ind) , data=social, + family = binomial, glmerControl(optimizer = "bobyqa"))</pre>						
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]						
Family: binomial (logit)						
Formula: feed ~ day + latency + (1 ind)						
Data: social						
Control: glmerControl(optimizer = "bobyqa")						
AIC BIC logLik deviance df.resid						
147.9 170.9 -65.9 131.9 124						
Scaled residuals:						
Min 1Q Median 3Q Max						
-2.2775 -0.3974 0.1138 0.3748 1.9095						
Random effects:						
Groups Name Variance Std.Dev.						
ind (Intercept) 8.178 2.86						
Number of obs: 132, groups: ind, 22						
Fixed effects:						

	Estimate	Std. Error	z value	Pr(> z)					
(Intercept)	-2.4646	1.1357	-2.170	0.03000	*				
day1	2.7231	1.0509	2.591	0.00956	**				
day3	3.6339	1.1417	3.183	0.00146	**				
day6	2.1658	1.0478	2.067	0.03872	*				
day10	3.2481	1.1005	2.952	0.00316	**				
day15	3.7163	1.1635	3.194	0.00140	**				
latency	0.2191	0.1303	1.682	0.09261	.				

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1									
Correlation of Fixed Effects:									
	(Intr)	day1	day3	day6	day10	day15			
day1	-0.621								
day3	-0.647	0.643							
day6	-0.649	0.627	0.638						
day10	-0.652	0.647	0.671	0.646					
day15	-0.656	0.644	0.675	0.643	0.673				
latency	-0.591	0.387	0.451	0.463	0.454	0.483			
> anova(lrfit202, lrfit200)									
Data: social									
Models:									
lrfit02: feed ~ day + latency + (1 ind)									
lrfit01: feed ~ day + bi + latency + (1 ind)									
	Df	AIC	BIC	logLik	deviance	Chisq	Chi	Df	Pr(>Chisq)
lrfit02	8	147.87	170.94	-65.936	131.87				
lrfit01	9	144.98	170.92	-63.489	126.98	4.8953		1	0.02693 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1									