

A Social Reinforcement Learning Hypothesis of Mutual Reward Preferences in Rats

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Abstract Although the use of neuroimaging techniques has revealed much about the neural correlates of social decision making (SDM) in humans, it remains poorly understood how social stimuli are represented, and how social decisions are implemented at the neural level in humans and in other species. To address this issue, the establishment of novel animal paradigms allowing a broad spectrum of neurobiological causal manipulations and neurophysiological recordings provides an exciting tool to investigate the neural implementation of social valuation in the brain. Here, we discuss the potential of a rodent model, *Rattus norvegicus*, for the understanding of SDM and its neural underpinnings. Particularly, we consider recent data collected in a rodent prosocial choice task within a social reinforcement framework and discuss factors that could drive SDM in rodents.

Keywords ■■■

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1 Social Decision Making: From Humans to Animals

Social decision making (SDM), i.e., choice behavior that directly or indirectly affects and/or is affected by others, is essential to navigate an ever more complex social environment. SDM is found in our desire to adopt a child and our decisions to give to charity or to punish social norm transgressions. A great amount of work has been devoted to outlining the behavioral dynamics underlying such decisions (Hastings et al. 2007; Wilson 2015), and a recent surge of interest has started to elucidate the general neural mechanisms underlying SDM in humans (Behrens et al. 2008; Izuma et al. 2008; Bhanji and Delgado 2013; Hernandez-Lallement et al. 2013; Ruff and Fehr 2014; Strombach et al. 2015).

Typically, studies exploring SDM in humans use noninvasive methods and correlative approaches (Rilling and Sanfey 2011; Crockett and Fehr 2014; Margittai et al. 2015). Although the use of such techniques has produced a formidable amount of data, the main limitation of these procedures is the lack of causal evidence for the contribution of a brain structure to SDM above and beyond the constraints of technologies available for human research (Knoch et al. 2006). As such, animal models of (social) decision making can complement human research at two different levels. First, they permit the use of neuroscientific methods that go beyond large-scale neural recording techniques in humans by providing direct access to neural activity with high temporal and spatial resolution, thus offering opportunities for causal interventions in the anatomy, activity, connectivity, genetics, and neurochemistry of the neural circuits implicated in SDM processes (Kalenscher and van Wingerden 2011). Second, through experimental analysis of behavior, such models provide a unique chance to compare the evolution of SDM across species (Crowley and Zentall 2013) and sample the spectrum of social behavior from markedly individualistic to highly social species. Therefore, animal models present essential tools to precisely delineate the neural pathways and mechanisms involved in SDM and provide a method to carry out between-species comparisons that are ultimately relevant for a better comprehension of human social cognition.

Up until now, the model of choice for investigating SDM is the nonhuman primate, representing a group of species closely related to humans (Silk and House 2011; Brosnan and de Waal 2014). Although such models are of great importance to study behavioral and evolutionary aspects of SDM, foremost ethical considerations limit their potential in neuroscientific research. Therefore, recent studies promote the use of rats (*Rattus norvegicus*) as an affordable, readily accessible, and standardized model to study SDM. There is a wealth of evidence suggesting that rodent decision making is often contingent on social contexts. For instance, social interaction modulates foraging behavior (Galef 1985; Galef and Whiskin 2008; Łopuch and Popik 2011) and motor learning (Zentall and Levine 1972), avoidance- (Masuda and Aou 2009) and fear-related behaviors (Kim et al. 2010; Atsak et al. 2011; Carrillo et al. 2015) as well as ultrasonic communication (Wöhr and Schwarting 2007; Wöhr et al. 2008; Łopuch and Popik 2011). Recent work demonstrates that rats reciprocate help to partners that previously helped them

(direct reciprocity; Rutte and Taborsky 2007a) and show generalized helping behavior if they received assistance from others in the past (generalized reciprocity; Pfeiffer et al. 2005; Rutte and Taborsky 2007b). Helping behavior is modulated by social experience, that is, actor rats help partners they have previously been in contact with (Ben-Ami Bartal et al. 2014) and might depend on the current satiation state (Schneeberger et al. 2012), bodily mass (Hernandez-Lallement et al. 2015), and food-seeking behavior of conspecifics (Márquez et al. 2015). Finally, it has recently been shown that rats, tested in a prosocial choice task (PCT), prefer options that yield food for themselves as well as for other individuals over alternatives yielding reward only to themselves, suggesting that rats' choices are driven by social factors beyond their own-payoff (Marquez and Moita 2012; Hernandez-Lallement et al. 2015). The growing interest in rodents as a model for social neuroscience is illustrated by the steady increase in the proportion of publications on neuroscientific aspects of social behavior in rats over the last decades (Fig. 1a). Interestingly, other rodent species have also received much attention (Fig. 1b) and have been shown to exhibit similar social preferences (Panksepp and Lahvis 2011; Lahvis et al. 2015). This is in contrast to a rather limited increase in the ratio of publications on social neuroscience in nonhuman primates (Fig. 1b). Note that ethical restrictions and different experimental timescales might account for these discrepancies; nonetheless, the growing importance of rodent models in this field is undeniable.

The translation of social behavior from humans to animal models is a complicated matter, and any claim of human-animal translation of supposed social motives should be supported by rigorous controls that establish the true “social” component of the observed behavior. For example, cooperative behavior emerged in pairs of rats trained in a small chamber (Daniel 1942) but disappeared when the chamber length increased (Daniel 1943) or when physical contact became impossible (Marcuella and Owens 1975). Similarly, empirical evidence suggests that food deprivation levels can influence the establishment of social behavior in rats (Taylor

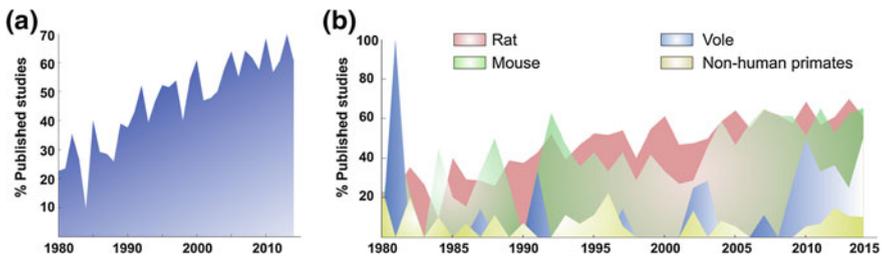


Fig. 1 Fraction of studies related to social behavior in different models indexed on Web of Science between 1980 and 2015. **a** Proportion of publications on the neuroscience of social behavior in rats in relation to the total number of studies on rat's social behavior ($Rat * Social * Neuroscience / Rat * Social$). **b**. Ratio between number of neuroscientific studies published on social behavior in a given animal model (rat, mouse, voles as rodents and macaques, chimpanzees, marmosets, cotton-top tamarin, and capuchin monkeys as nonhuman primate) and all studies using the same model published on social behavior ($Model * Social * Neuroscience / Model * Social$)

1975; Viana et al. 2010), higher deprivation levels resulting in decreased prosocial behavior. Finally, a decrease of social learning rate (Bunch and Zentall 1980) and cooperative moves (Gardner et al. 1984) is observed after abolishment of visual communication, thus suggesting that sensory and physical aspects of the experimental setup can have radical effects on putative social behavior. Thus, depending on task contingencies, experimental designs, physical setup and/or sensory communication possibilities, nonsocial cues might compete with social cues to affect decision making in social contexts. For instance, the establishment of cooperative coordination increases in pairs of rats when mediated by a nonsocial light cue, but not in the absence of the cue and furthermore disappears when reward is delivered for own instrumental behavior (Schuster 2002). These results emphasize the importance of including controls for nonsocial sources of behavioral reinforcement in experiments investigating social behavioral dynamics and mechanisms. Importantly, such nonsocial controls could reveal a relevant baseline behavioral (choice) pattern (not necessarily equivalent to economically defined indifference between the outcomes; Hernandez-Lallement et al. 2015) to which behavior in the social condition could be contrasted.

2 A Social Reinforcement Learning Framework for Understanding Social Decision Making in Animals

Animal choice behavior is often analyzed within a reinforcement learning framework (Schultz 2006). According to the most basic reinforcement learning principles, action–outcome contingencies are learned through positive reinforcement (i.e., the likelihood of an operant behavior increases if it is followed by a reward) and/or negative reinforcement (i.e., the likelihood decreases if it is followed by an aversive event, such as an electric shock; Niv and Montague 2008). SDM has been recently discussed in the light of a *social* reinforcement hypothesis (Chang et al. 2011; Hernandez-Lallement et al. 2015, 2016) which states that animals' choices in social contexts are also affected by a process that updates the likelihood of some actions over alternative courses of action based on *social* outcomes. According to this view, any behavior that results in a social outcome that is perceived as appetitive, e.g., a friendly smile in humans, or putatively rewarding communication signals emitted by rats (Willuhn et al. 2014), will be reinforced. Correspondingly, any behavior that results in a social outcome that is perceived as aversive (e.g., swearing in humans) or negative (e.g., aggressive reactions of conspecifics in nonhuman animals) will less likely be repeated in the future. In the social reinforcement framework, social reinforcers are thus social stimuli that carry positive or negative reinforcement properties. There is indirect evidence for this hypothesis in rats. For instance, putatively rewarding 50 kHz ultrasonic vocalizations (USVs; see below) emitted by a conspecific rat trigger dopamine release in an observer rat's nucleus accumbens (NAcc; Willuhn et al. 2014), a signal associated with reinforcement learning

(Schultz et al. 1997). Furthermore, witnessing a reward delivered to a conspecific rat elicits activation in an observer’s NAcc—a possible mechanism for vicarious reinforcement (Kashtelyan et al. 2014).

Recently, we used this framework to discuss the dynamics of prosocial choice behavior in a rodent PCT (Fig. 2a; Hernandez-Lallement et al. 2015, 2016). In this task, pairs of rats (an actor and a partner) are trained in a double T-maze setting. Actors are the first movers and choose to enter one of two different compartments, either choice leading to an identical reward for themselves. However, entering one compartment triggers the delivery of an additional reward for the partner rat (both-reward, BR; Fig. 2a, upper panel), whereas entering the alternative compartment does not yield any additional reward to the partner (own reward, OR; lower panel). To control for nonsocial secondary reinforcement effects, actor rats

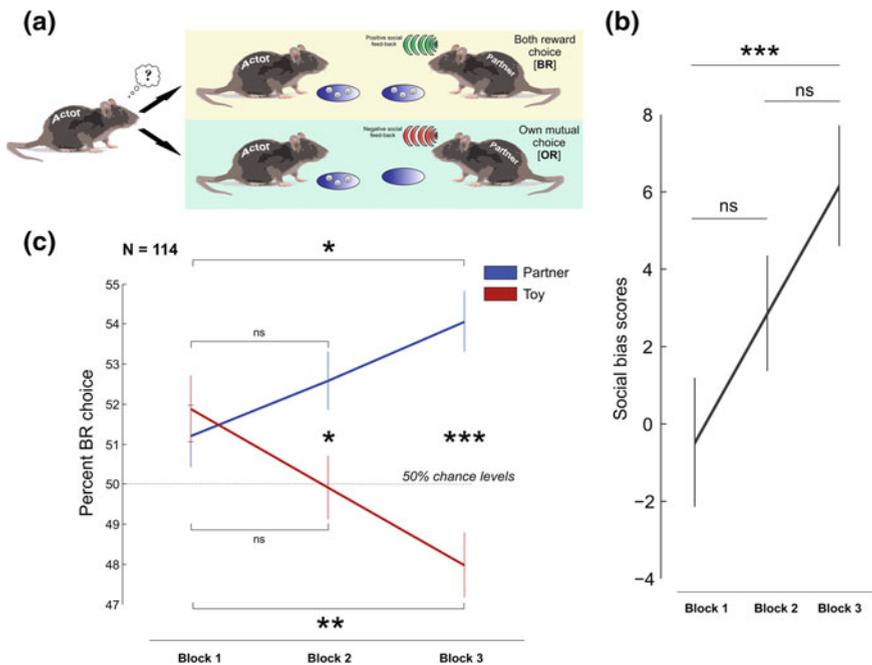


Fig. 2 Social reinforcement learning framework. **a** Putative reinforcement mechanisms in a prosocial choice task for rodents. An actor rat decides between rewarding (upper panel, yellow background) and not rewarding (lower panel, mint background) a partner rat at no cost to himself while being identically rewarded for both choices as well. The reinforcement learning hypothesis implies that both outcomes can lead to positive and negative social feedback from the partner in case it gets access to food (upper panel), or not (lower panel), respectively. **b** Social bias scores increased within sessions. Social bias score computed across 114 rats, eight sessions, and blocks of five trials. The distributions increased over blocks and became significantly different from the precedent block from block 2 onwards. **c** %BR preference increased and decreased in the partner and toy conditions, respectively. Preference for the BR alternative increased steadily across trials within sessions in the partner condition and decreased in the toy condition. Error bars are s.e.m. * $p < .05$; *** $p < .001$, ns not significant; Bonferroni corrected

are also tested in a nonsocial toy condition. In this control condition, the partner rat is replaced by a toy animal of similar shape and size, while keeping all other task parameters identical to the social condition, including the reward contingencies. Animals are allowed to sample both BR- and OR-outcomes for a certain number of forced trials (only one option available to the actor) followed by free choice trials (the actor can choose freely between OR- and BR-options) where their social preferences can be observed. Results show that rats prefer mutual rewards more in the partner condition than in the toy control condition (Hernandez-Lallement et al. 2015). We interpreted this behavior as evidence for prosocial preference in rats because the actors' inclination for providing food access to the partners was driven by social factors beyond their own-payoff.

The social reinforcement learning hypothesis provides a useful and parsimonious framework that equips us with conceptual tools to describe and predict the rats' behavior in the PCT task. As pointed out, an actor's prosocial choice could be driven by (i) the consequence of positive social reinforcement (Fig. 2a, "*Positive social feedback*"), e.g., rewarding communication signals emitted by the partner (Seffer et al. 2014) or pleasure derived from eating rewards in spatial proximity (Barnett and Spencer 1951). Additionally, behavior could also be reinforced by (ii) negative social reinforcement (Fig. 2a, "*Negative social feedback*"), e.g., potential distress signals produced by partners (Kim et al. 2010; Atsak et al. 2011) missing out on reward in OR choices. As previously noted (Hernandez-Lallement et al. 2015), positive and negative social reinforcement are not mutually exclusive, but could act in concert to reinforce prosocial choices. If the social reinforcement hypothesis accounts for the choice allocation observed in the PCT, one should be able to find signatures of social learning in the choice dynamics of actor rats. To search for signs of social learning, we exploited the reversal nature of the PCT task. Briefly, to control for side biases and habit formation, the compartments associated with BR- and OR-outcomes were pseudo-randomized across testing sessions and rats. Thus, on nearly every session, the OR/BR-compartment assignments were reversed with respect to the previous session, and animals had to re-learn the compartment-outcome contingencies anew. It is important to note again that the outcome for the actor was identical for both choices; OR- and BR-choices differed only in the outcome to the partner rat. Hence, flexible adaptation to the frequent contingency reversals could only be driven by the social reinforcing component of BR-outcomes, not by absolute differences in outcomes. Using a large data set of rats tested on the PCT ($N = 114$ rats; data taken from different, partly unpublished experiments), we divided the first eight sessions of testing (the number of training sessions differed across rats and experiments, but each animal in the data set was trained for at least 8 sessions per condition) in three blocks of five trials (each session consisted of 15 trials, which we subdivided into three blocks of five trials for analysis) and computed mean social bias scores across animals. Social bias scores quantify the normalized difference in mutual reward choices between partner and toy conditions, i.e., how much more (or less) an actor chooses the BR-option in the partner- compared to the overall BR preference levels. Social bias scores can be construed as the added social value of a conspecific's access to food

(See Hernandez-Lallement et al. 2015 for similar computation). The social bias score for rat i was computed with the following equation:

$$SB_i = \frac{BR(\text{partner})_i - BR(\text{toy})_i}{BR(\text{partner})_i + BR(\text{toy})_i} * 100 \quad (1)$$

Note that in previous studies (Hernandez-Lallement et al. 2015, 2016), we used the BR preference in toy condition only in the denominator term of the social bias score equation which captured more directly the percent change from toy baseline levels. However, using only the percent change in the toy condition as normalization could potentially yield skewed distributions.¹ The formula used here, which produces strictly normalized values located between -100 and 100 %, yields qualitatively similar results while retaining a normal distribution of social bias scores at the population level. Accordingly, a positive social bias score for rat i (SB_i), i.e., higher BR preference in the partner than in the toy condition, reflects the added positive social value for a conspecific's access to food, whereas a negative social bias score can be interpreted as negative social value. Results are depicted in Fig. 2b. A repeated-measures ANOVA revealed a significant main effect of blocks on social bias scores ($F_{(2,226)} = 10.42$, $p < .001$, $\eta_p^2 = .08$), indicating that social preferences (re-)emerged across trials within sessions. Post hoc pairwise comparisons showed a significant increase in social bias scores between blocks 1 and 3 ($t_{(113)} = 4.45$, $p < .001$; $CI_{99} = [-10.55, -2.73]$; Cohen's $d = .54$; Bonferroni corrected; $\alpha = .02$), whereas no significant difference was found between blocks 2 and 3 ($t_{(113)} = 2.26$, $p = .03$; $CI_{99} = [-7.14, .54]$; $d = .28$) as well as between blocks 1 and 2 ($t_{(113)} = 2.38$, $p = .02$; $CI_{99} = [-7.02, .34]$; $d = .28$).

Importantly, social bias scores quantify the normalized difference in BR preference between partner and toy condition (see Eq. 1). Therefore, to break down the processes underlying the increase of social bias scores previously reported, we computed the average fraction of BR-choices for the partner (blue) and toy (red) conditions, i.e., the percentage of BR-choices out of all choices (Fig. 2c). We found that rats were nearly indifferent between OR- and BR-alternatives at the beginning of a partner session, but their preferences for BR- over OR-options in the partner condition became increasingly pronounced as the session progressed. Surprisingly, this pattern was completely reversed in the toy condition, where animals decreased their preferences for BR over OR choices across trials within sessions. A repeated-measures ANOVA (with condition and block as within-subject factors) revealed a significant effect of condition on %BR-choices ($F_{(1,113)} = 13.23$, $p < .001$, $\eta_p^2 = .11$) and a significant condition * block interaction ($F_{(2,226)} = 10.62$, $p < .001$, $\eta_p^2 = .09$). Further post hoc pairwise comparisons revealed a significant difference in %BR-choices between partner and toy condition for block 2 as well as block 3 (paired-samples t test; Block 2: $t_{(113)} = 2.54$, $p < .05$, $CI_{99} = [-.09, 5.62]$; $d = .34$; Block 3: $t_{(113)} = 5.53$, $p < .001$, $CI_{99} = [3.23, 9.05]$; $d = .74$, Bonferroni

¹This was not the case in previous studies from Hernandez-Lallement et al. 2015, 2016.

corrected), but not in block 1 ($t_{(113)} = -.51, p = .58, CI_{99} = [-3.78; 2.55]; d = -.07$). Moreover, %BR-choices were significantly different between blocks 1 and 3 in both partner ($t_{(113)} = 3.00, p < .05, CI_{99} = [-.37, -5.40]; d = .35$) and toy conditions ($t_{(113)} = 3.61, p < .01, CI_{99} = [6.68, 1.06]; d = .44$). No additional significant differences were found between the blocks.

These findings have two important implications. First, they show that preference for the BR-option increased across trials in the partner sessions, a process which might reflect the updating of the social value of the choice outcomes. Second, we observed a within-session decrease of BR preference in the toy condition which suggests that animals developed an aversion against additional rewards delivered to the opposite compartment in a nonsocial context, possibly reflecting frustration effects related to rats' inability to access uneaten rewards in the opposite compartment. This bifurcating pattern implicates that "baseline" preference levels in the PCT are dynamic; the actual preference for social outcomes should, therefore, not be compared to indifference levels (50 %), but rather to the BR-choice levels observed in the nonsocial context control condition. This is precisely why social bias scores, i.e., the percent change of BR-choice between partner and toy condition, in our opinion is a better estimate of mutual reward preferences than comparison of BR-choices against chance. Overall, these data are consistent with the idea that the emergence of rats' social preferences reflects social learning.

3 Individual Differences in Social Learning

An identical social context might affect individual animals in different ways. For instance, social behavior in rats seems to be differentially influenced by group hierarchy (Baenninger 1966) or social experience (Ben-Ami Bartal et al. 2014). Such inter-individual differences in social behavior should be prominent in PCT performance, too. To characterize individual differences in social preferences, we compared individual social bias scores to a bootstrapped reference distribution obtained through random permutation. Briefly (See Hernandez-Lallement et al. 2015 for exact procedure), we generated a distribution of permuted social bias scores, computed by drawing scores (with replacement, $N = 5000$ times) from sessions in both partner and toy conditions while shuffling the session labels. We then compared actual social bias scores to the 95 % confidence interval on this simulated distribution of social bias scores (Fig. 3a; confidence interval limits: $[-2.66; 2.66]$). Animals with social bias scores exceeding the upper limit of the confidence interval were categorized as "prosocial" ($n = 55; 48\%$ of all animals), whereas all remaining animals were categorized as "nonsocial" ($n = 59; 52\%$). Strikingly, in comparison with baseline levels (toy condition), prosocial animals had between 2 to nearly 21 more BR-choices in the partner compared to the toy condition, illustrating that social preference levels varied substantially, even within the category of rats classified as prosocial. Additionally, animals classified as nonsocial included those that showed rather indifferent choice allocations across

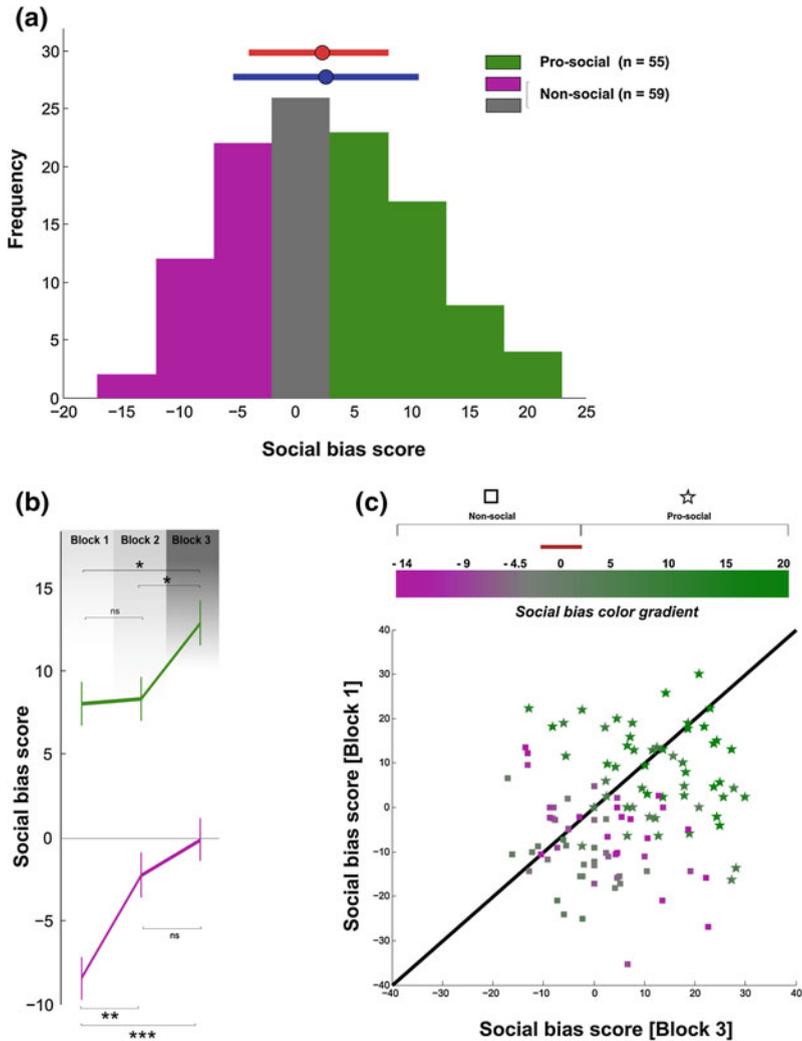


Fig. 3 Individual differences in prosocial choice. **a** Individual differences in social learning. Histogram of social bias scores. Social bias scores exceeding the upper limit of confidence interval (upper limit: 5.47) were categorized as “prosocial” (green; $n = 55$; 48 % of all rats) and remaining animals were categorized as “nonsocial” (violet/gray; $n = 59$, 52 % of all rats). The gray bar represents animals from the nonsocial group located within the 95 % confidence interval. Blue dot and line are the mean and standard deviation of the social bias score distribution, respectively. Red dot and line are the distribution’s median and the 25 and 75 % percentile values, respectively. **b** Average social bias scores across blocks for prosocial (green) and nonsocial groups (violet). Both groups showed significant increase in social bias score across blocks. **c** Increasing social bias scores from block 1 to block 3. Scatter plot of individual social bias scores levels in block 1 (y-axis) and block 3 (x-axis) for prosocial (star) and nonsocial animals (squares). Data points under the diagonal represent animals that had an increase in social bias score from block 1 to block 3. Color gradient inform on overall social bias score values (See panel a). The red horizontal line represents the 95 % confidence interval. Error bars are s.e.m. * $p < .05$; ** $p < .01$; *** $p < .001$, ns not significant; Bonferroni corrected

conditions (SB within the bootstrapped confidence interval; Fig. 3a, gray bar) and others that even showed “antisocial²” behavior, i.e., negative social bias scores reflecting lower BR preferences for a conspecific than for inanimate toys. Note that negative social bias scores reached only modest levels compared to the positive social bias scores of the prosocial group.

In order to further investigate whether nonsocial animals truly showed overall indifference and/or aversion toward mutual rewards across trials, we computed social bias scores in each block of trials for both prosocial and nonsocial groups. We hypothesized that, contrary to prosocial animals, rats in the nonsocial group would not show significant change in social bias scores across blocks (Fig. 3b). A repeated-measures ANOVA (blocks and group as within- and between-subject factors, respectively) revealed a significant main effect of block on social bias scores ($F_{(2,224)} = 10.25, p < .001, \eta_p^2 = .08$), as well as a significant block * group interaction ($F_{(2,224)} = 4.07, p < .05, \eta_p^2 = .04$). Moreover, there was a significant difference in social bias scores between blocks 1 and 3 ($t_{(54)} = 2.21, p < .05, CI_{99} = [-10.72, 1.01]; d = .47$) as well as 2 and 3 in the prosocial group ($t_{(54)} = 2.07, p < .05, CI_{99} = [-10.44, 1.32]; d = -.44$), but not between blocks 1 and 2 ($t_{(54)} = .15, p = 1.00, CI_{99} = [-5.65, 5.06]; d = .03$), confirming that prosocial animals showed social learning. However, and crucially, we also found a significant difference in social bias scores between blocks 1 and 2 ($t_{(58)} = 3.17, p < .01, CI_{99} = [-11.27, -1.09]; d = -.63$) as well as between blocks 1 and 3 ($t_{(58)} = 4.00, p < .001, CI_{99} = [-12.70, -2.91]; d = -.87$) in the nonsocial group, although no difference was found between blocks 2 and 3 ($t_{(58)} = -.95, p = .74, CI_{99} = [-7.33, 3.09]; d = -.22$). These results suggest that animals initially classified as nonsocial also showed social learning. While 64 % of prosocial animals ($n = 35$) increased their social bias scores from blocks 1–3 (Fig. 3c; stars under the diagonal), 70 % of nonsocial animals ($n = 41$) showed a similar increase (squares under the diagonal), adding further support to the notion that nonsocial animals showed social learning, too. Therefore, although overall mean social bias scores differed between groups, the social learning rate might have been comparable across animals in both groups. To address this possibility, we computed the absolute difference in social bias scores between blocks 1 and 3 for every animal in each group. Direct comparison showed that rats in both groups showed comparable increases in social bias scores from block 1 to block 3 (Fig. 4a; $t_{(112)} = -1.16, p = .25; CI_{95} = [-9.35, 2.47], d = -.21$). Overall, this analysis suggests that animals classified as prosocial or nonsocial differed predominantly in their baseline social preference levels rather than in social learning capabilities, which were robust across the whole population.

While the increase in social bias scores across blocks was comparable between groups, it is conceivable that prosocial and nonsocial animals differed in their social learning rate *within* the partner and the toy conditions. To address this possibility,

²The term “antisocial” needs to be interpreted with caution, because rats’ choices may have been motivated by nonsocial factors that were unrelated to malicious, egocentric, or other “antisocial” motives. We use the term “antisocial” agnostically to describe the negative effect of social context on social preferences.

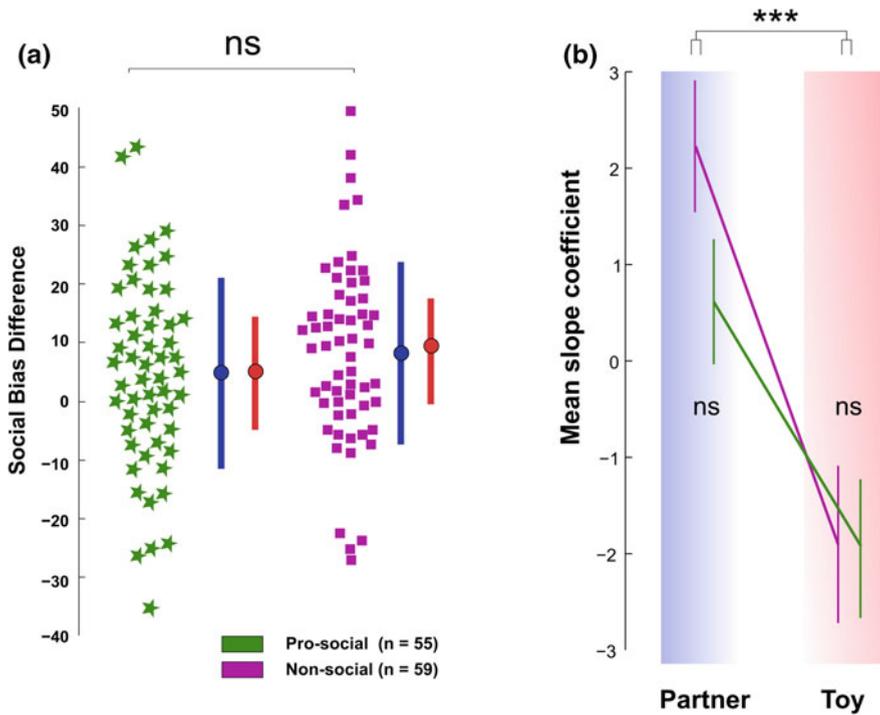


Fig. 4 Individual differences in prosocial choice. **a** Magnitude of change in social bias score between the blocks. There was no significant difference in social bias score difference (Block 3–Block 1) between prosocial (*green*) and nonsocial groups (*violet*). *Blue dot and line* are the distribution’s mean and standard deviation, respectively. *Red dot and line* are the distribution’s median and the 25 and 75 % percentile values, respectively. **b** Slope coefficient for %BR across blocks per group in the partner (*blue background*) and toy conditions (*red background*). While both groups showed higher slope coefficients in the partner than in the toy condition (main effect of condition), there was no difference between groups in either condition. Error bars are s.e.m. *** $p < .001$, ns not significant

we regressed, for each condition separately, the rats’ individual %BR-choices against block and extracted the individual regression coefficients as estimates of the steepness of the slopes across blocks as a proxy of the rats’ learning rates (linear fit of the %BR in each block, per animal; steeper slopes indicate higher learning rates). A mixed ANOVA revealed a significant effect of condition ($F_{(1,112)} = 20.01$, $p < .001$, $\eta_p^2 = .15$), but not in the condition * group interaction ($F_{(1,112)} = 1.23$, $p = .27$, $\eta_p^2 = .01$). While both groups showed significantly higher slope values in the partner than in the toy condition (prosocial: $t_{(112)} = 2.28$, $p < .05$; $CI_{99} = [-.43, 5.47]$, $d = .46$; nonsocial: $t_{(112)} = 4.12$, $p < .01$; $CI_{99} = [1.47, 6.88]$, $d = .77$), slope coefficients did not differ between groups in either condition (partner: $t_{(112)} = 1.69$, $p = .10$; $CI_{99} = [-.89, 4.11]$, $d = -.31$; toy: $t_{(112)} = -.05$, $p = .96$; $CI_{99} = [-2.88, 2.77]$, $d = .01$). Thus, this analysis also confirms that both prosocial and nonsocial animals showed comparable social learning in each condition.

Altogether, these results show that prosocial and nonsocial rats show comparable social reinforcement learning capabilities and that individual differences in initial social preference levels between animals can account for differences in prosocial preferences observed at the group level. Thus, considering learning rates next to preference levels is advisable when investigating social choice behavior in rodents. Regarding the PCT, one challenge for future research is to determine whether animals initially classified as nonsocial, i.e., rats that had lower social bias scores to begin with, would reach similar levels of mutual reward preferences as prosocial rats if they were trained more extensively. This possibility remains to be investigated.

4 Potential Mediators of Social Reinforcement

Although consistent with the social reinforcement hypothesis, the results presented above do not inform on what kind of social reinforcement, negative and/or positive, underlies the within-session increase of BR-preference. Several social stimuli could drive the rats' choice allocation in the PCT. Prime candidates are auditory stimuli, mainly USVs, that are known to carry affective state information (Knutson et al. 1999; Litvin et al. 2007) not only in rodents (Burgdorf et al. 2008; Wöhr and Schwarting 2008; Seffer et al. 2014) but also in other species (Sharp et al. 2005; Gadziola et al. 2012a). Notably, substantial evidence obtained in big brown bats suggest that amygdala neurons discriminate between different social USVs (Naumann and Kanwal 2011; Gadziola et al. 2012b; Peterson and Wenstrup 2012; Grimsley et al. 2013). Similar results were obtained in rats showing that USVs reflecting negative (22 kHz) and positive (50 kHz) affective state can modulate approach behavior (Wöhr et al. 2008) and are coupled to tonic increase and decrease of amygdala neuron firing rates, respectively (Parsana et al. 2012). Finally, the fact that 50 kHz USVs elicit phasic dopamine release in the nucleus accumbens (Willuhn et al. 2014), as mentioned above, is consistent with the idea that USVs have social significance and qualify as social reinforcers. Other stimuli, such as odors (Wang et al. 2006; Wesson 2013) might also carry reinforcing properties for rats. However, the idea that olfaction would drive prosocial choice allocation in the PCT would require highly dynamic chemical processes, which we believe unlikely given the trial-based design. Assessing the influence of several putative social signals in transmitting partner feedback and their effect on SDM remains an unresolved issue for now.

Recent evidence showing that lesion to the basolateral amygdala (BLA) abolishes mutual reward preferences in rats (Fig. 5; Hernandez-Lallement et al. 2016) sheds light on the potential neural bases of mutual reward preferences. The BLA, a neuronal cluster located in the temporal lobe involved in associative (social) learning (Adolphs 2009), receives strong innervations from visual, auditory, and somatosensory tracts, as well as from olfactory and vomeronasal pathways in rodents, and is therefore often considered as the amygdala sensory interface

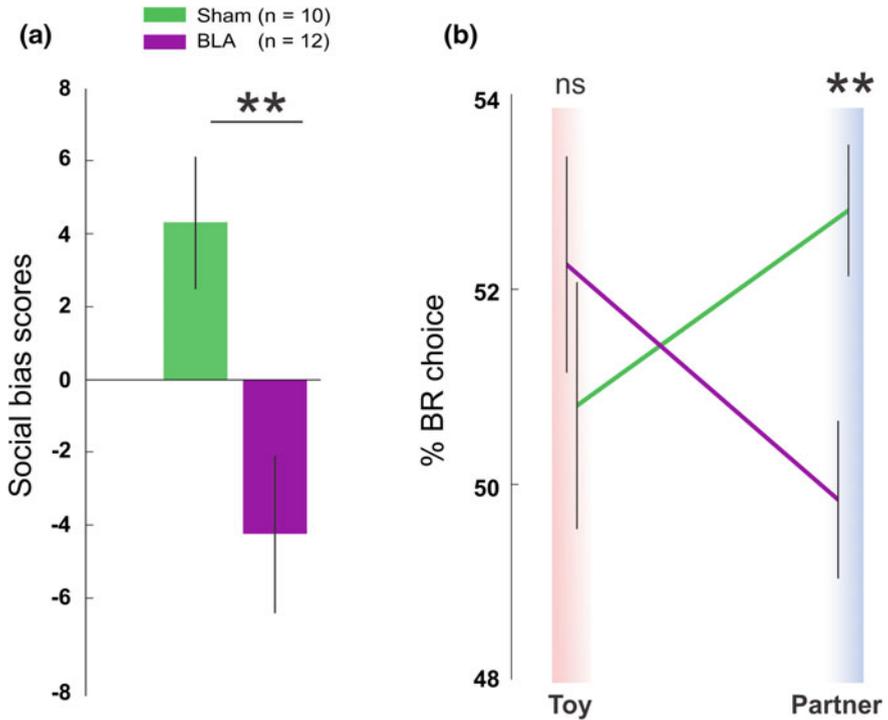


Fig. 5 Basolateral amygdala lesions impair mutual reward preferences in rats. **a** Social bias scores in sham-operated (*green*) and BLA-lesioned groups (*violet*). BLA-lesioned animals had significantly lower social bias scores than sham-operated animals. **b** Percentage of mutual reward choices for sham (*green*) and BLA group (*purple*). In comparison with sham-operated animals, BLA-lesioned rats made significantly less mutual reward choices in the partner but not the toy condition. *Shading* blue partner; red toy condition. Error bars represent the standard error of the mean, s.e.m. ** $p < .01$, independent-samples t test; Bonferroni corrected; *ns* not significant. All panels were adapted with permission from Hernandez-Lallement et al. 2016

(Phelps and LeDoux 2005; Brennan and Kendrick 2006). Particularly, it has been proposed that the BLA may act as a vigilance device important for linking the incentive properties and outcome values of rewards and punishments to predictive sensory cues, and enhancing their affective salience (Schoenbaum et al. 1999, 2003). Accordingly, the BLA might sensitize individuals to the emotional value of social information and thus contribute to social learning (Adolphs 2009). Thus, BLA lesion-related impairments in the establishment of mutual reward preferences could reflect a deficit in rodent decision making in the social domain, reminiscent of similar deficits in human populations with impaired amygdala function (Adolphs 2010; Decety et al. 2013).

In conclusion, we believe that the emergence of rodent models of SDM within a social reinforcement learning framework provides exciting opportunities to study social choice using the full range of the neurobiological toolbox. Novel behavioral

paradigms such as the PCT and others (Márquez et al. 2015) pave the way toward a mechanistic model of social preferences and therefore contribute to a better understanding of the neural circuits involved in nonhuman and human SDM.

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