

# LIFE NATURE SOCIETY



# Behavioral and neural basis of inequity aversion in rats

Tobias Kalenscher

*Oxford, May 2018*

# Prosocial behavior

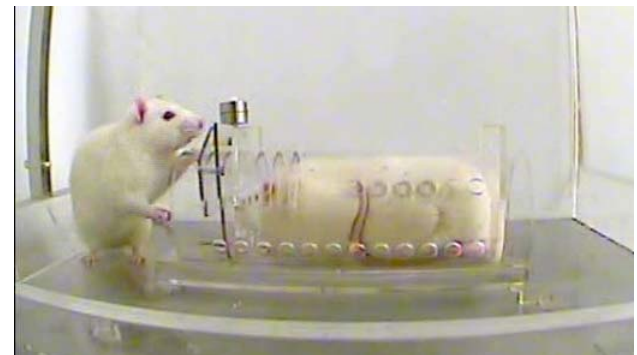


*Savage Chickens*

by Doug Savage



[www.savagechickens.com](http://www.savagechickens.com)









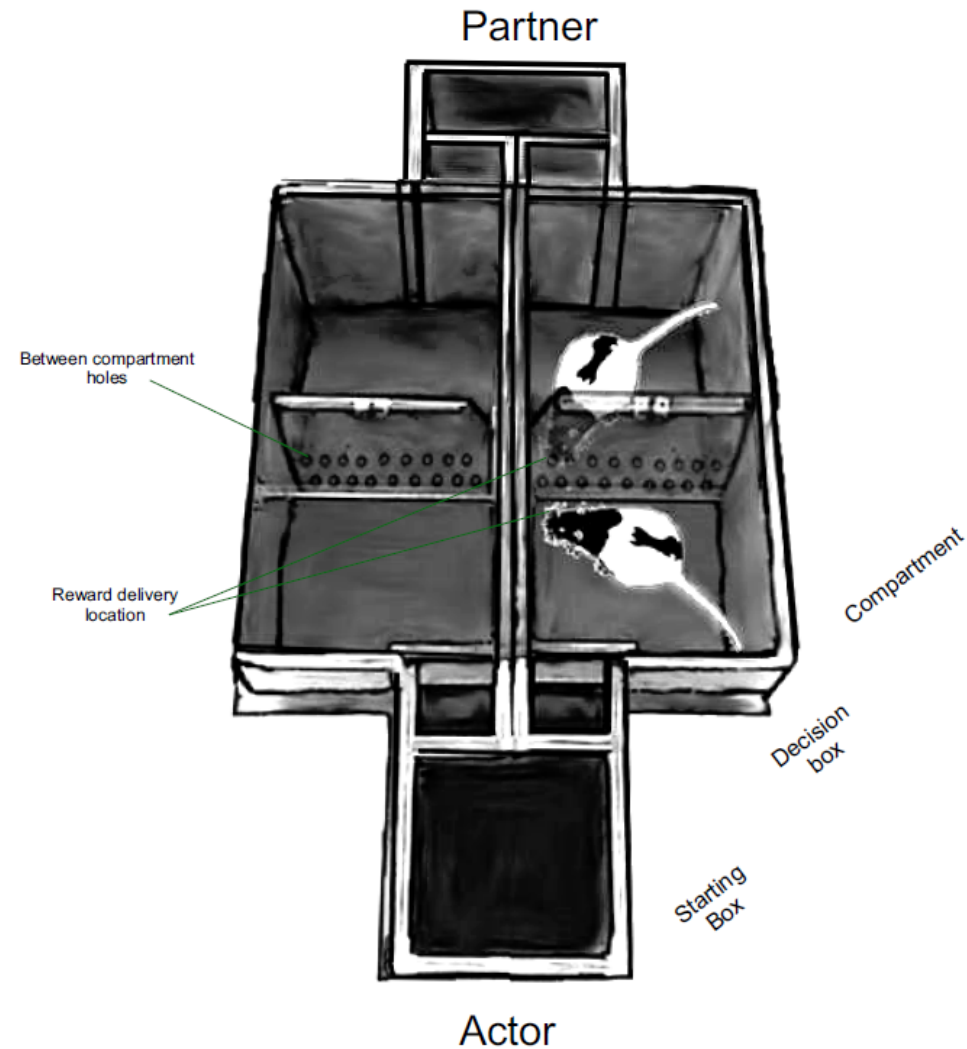
- **Inequity aversion:** behavioural response to an unequal reward distribution, given equal efforts to produce the reward
- **Advantageous inequity aversion (compassion):** sensitivity to unfair reward distributions that leave the decision-maker better-off
- **Disadvantageous inequity aversion (envy):** sensitivity to unfair reward distributions that leave the other better-off



**Do rats show *advantageous*  
inequity aversion?**



# The Rodent Prosocial Choice Task

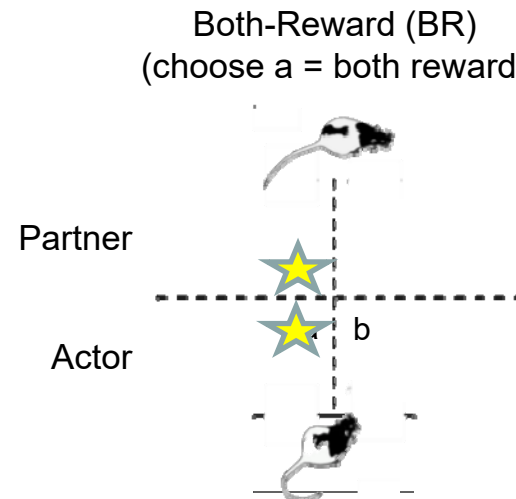


*Hernandez-Lallement et al., 2015*

# The Rodent Prosocial Choice Task

## Social condition:

- One compartment randomly assigned as 'Both-Reward (BR)' (a), the other as 'Own-Reward (OR)' compartment' (b)
- Actor is first mover
- Partner is directed to opposite compartment
- *Both-Reward (BR)*: if actor enters 'BR-compartment' (a), both rats receive reward



*Hernandez-Lallement et al., 2015*



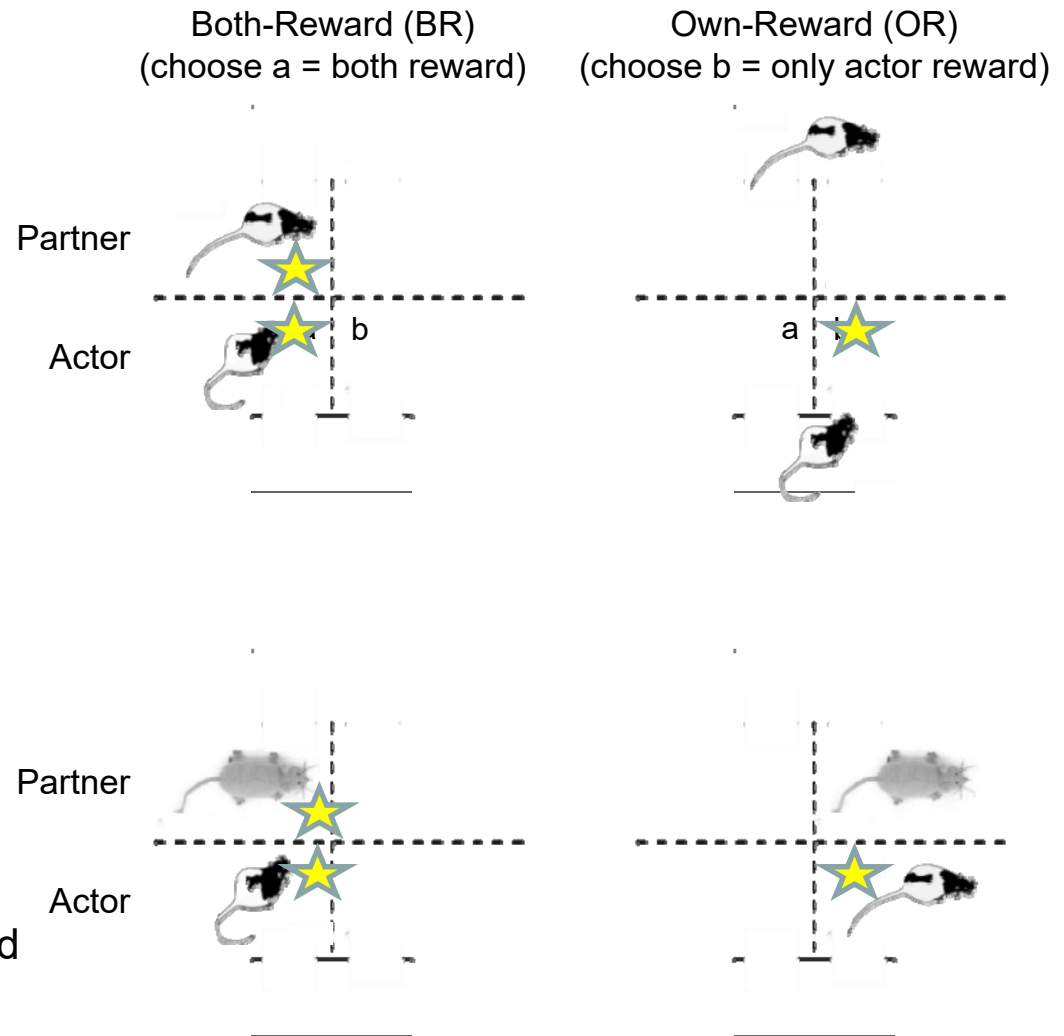
# The Rodent Prosocial Choice Task

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- Actor is first mover
- Partner is directed to opposite compartment
- *Both-Reward (BR)*: if actor enters 'BR-compartment' (a), both rats receive reward
- *Own-Reward (OR)*: if actor enters 'OR-compartment' (b), only actor receives a reward (same reward and delay as in compartment a)

## Non-social control:

- Same as social condition, incl. reward
- But partner rat is replaced by toy rat

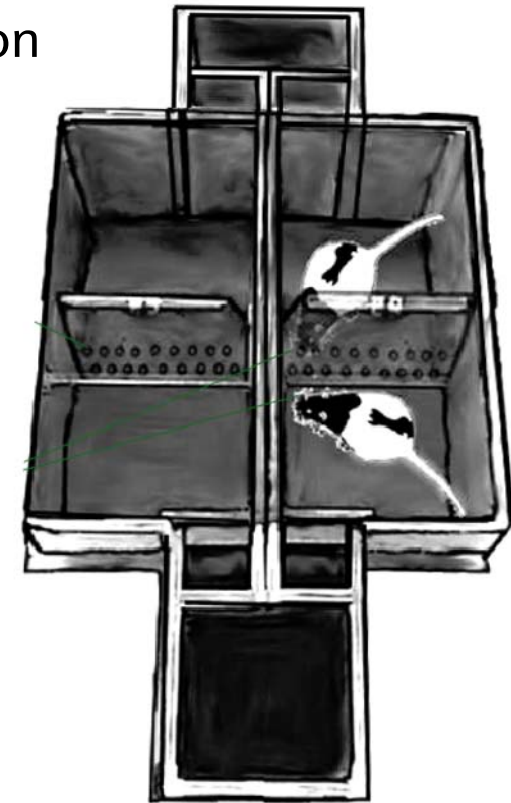


Hernandez-Lallement et al., 2015

# The Rodent Prosocial Choice Task

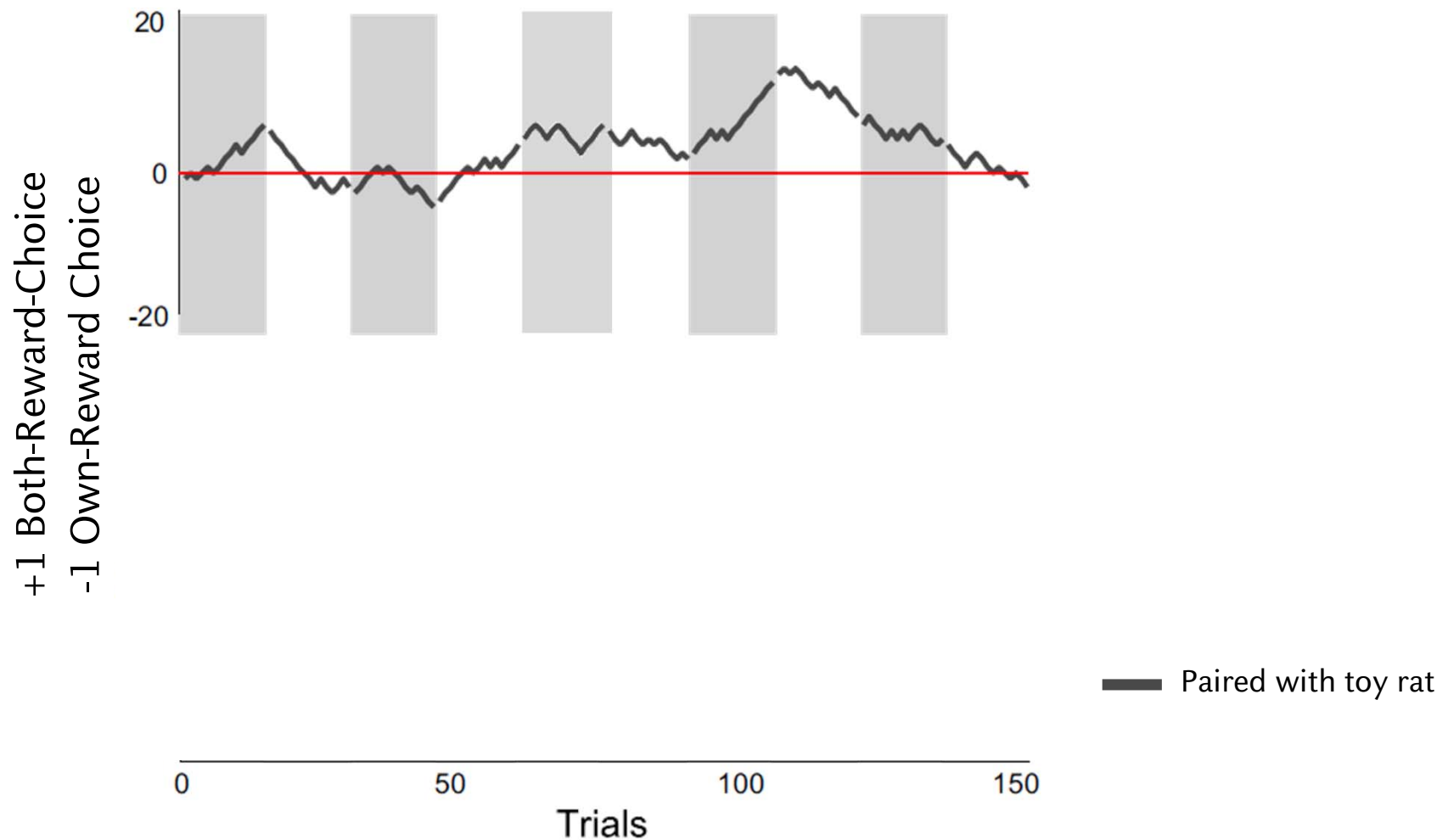
## Design

- By now, data from more than 120 rats
  - Here: data from 48 animals
- 10 sessions in partner + 10 sessions in toy condition
- 10 forced-choice + 25 free-choice trials per session
- Side of both-reward and own-reward-compartments pseudo-randomized across rats and sessions
  - Frequent reversals
- Start box and condition (toy vs. partner) also pseudo-randomized



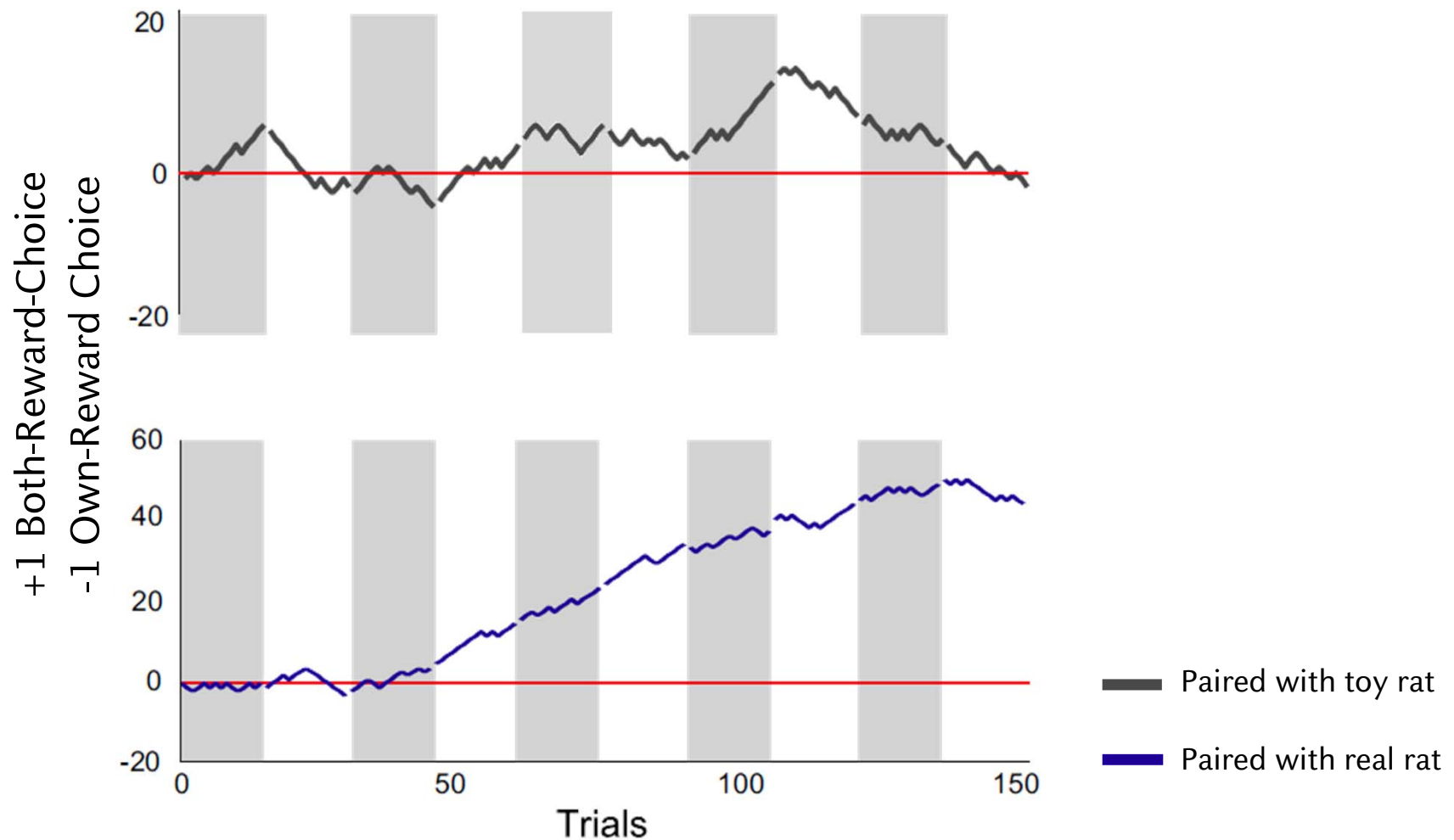


# The Rodent Prosocial Choice Task



*Hernandez-Lallement et al., 2015*

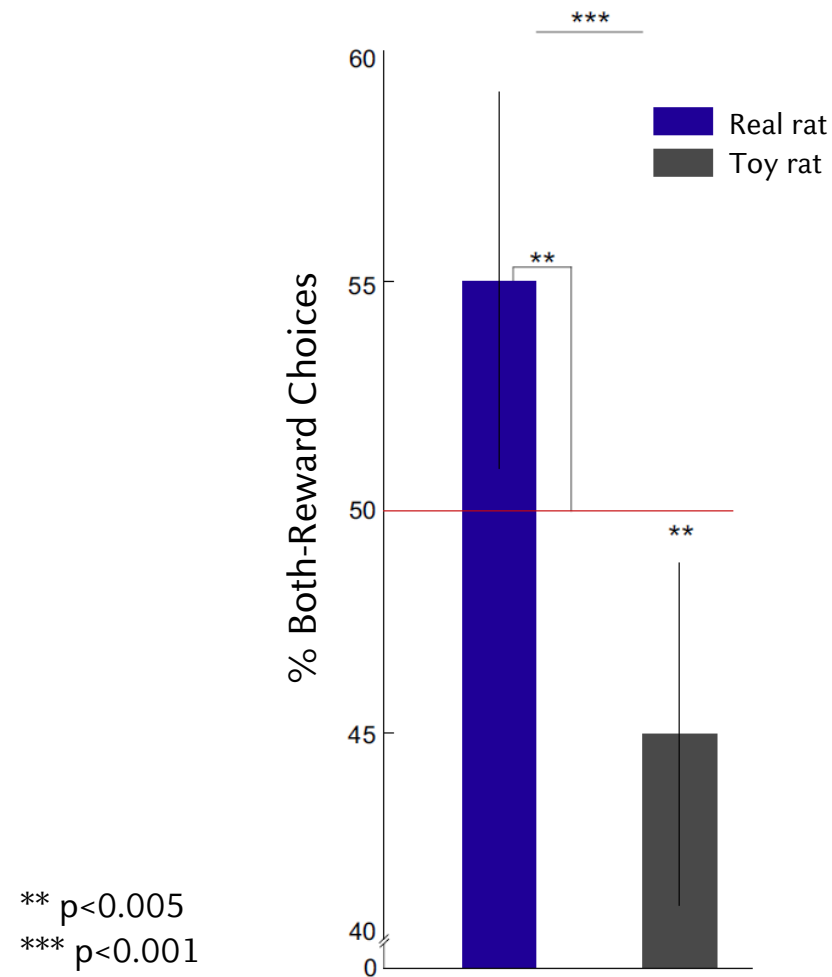
# The Rodent Prosocial Choice Task



*Hernandez-Lallement et al., 2015*

# The Rodent Prosocial Choice Task

## Both-Reward Choices



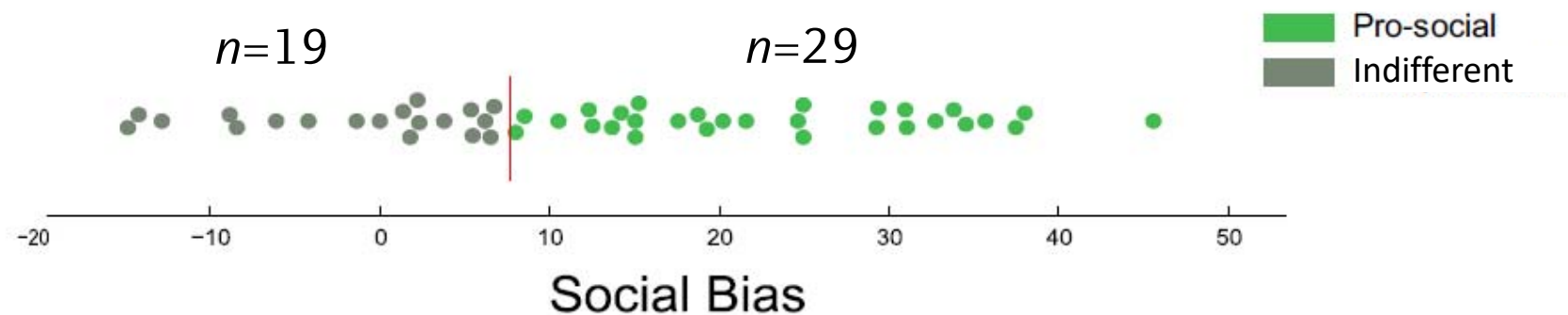
*Hernandez-Lallement et al., 2015*

## Individual Differences in *Both-Reward* Preferences

- Social Bias Score for rat  $i$ : percent-difference in both-reward (#BR) choices between partner- and toy-condition

$$\text{Social Bias Score}_i = \left[ \frac{\#BR(\text{partner})_i - \#BR(\text{toy})_i}{\#BR(\text{toy})_i} \right] * 100$$

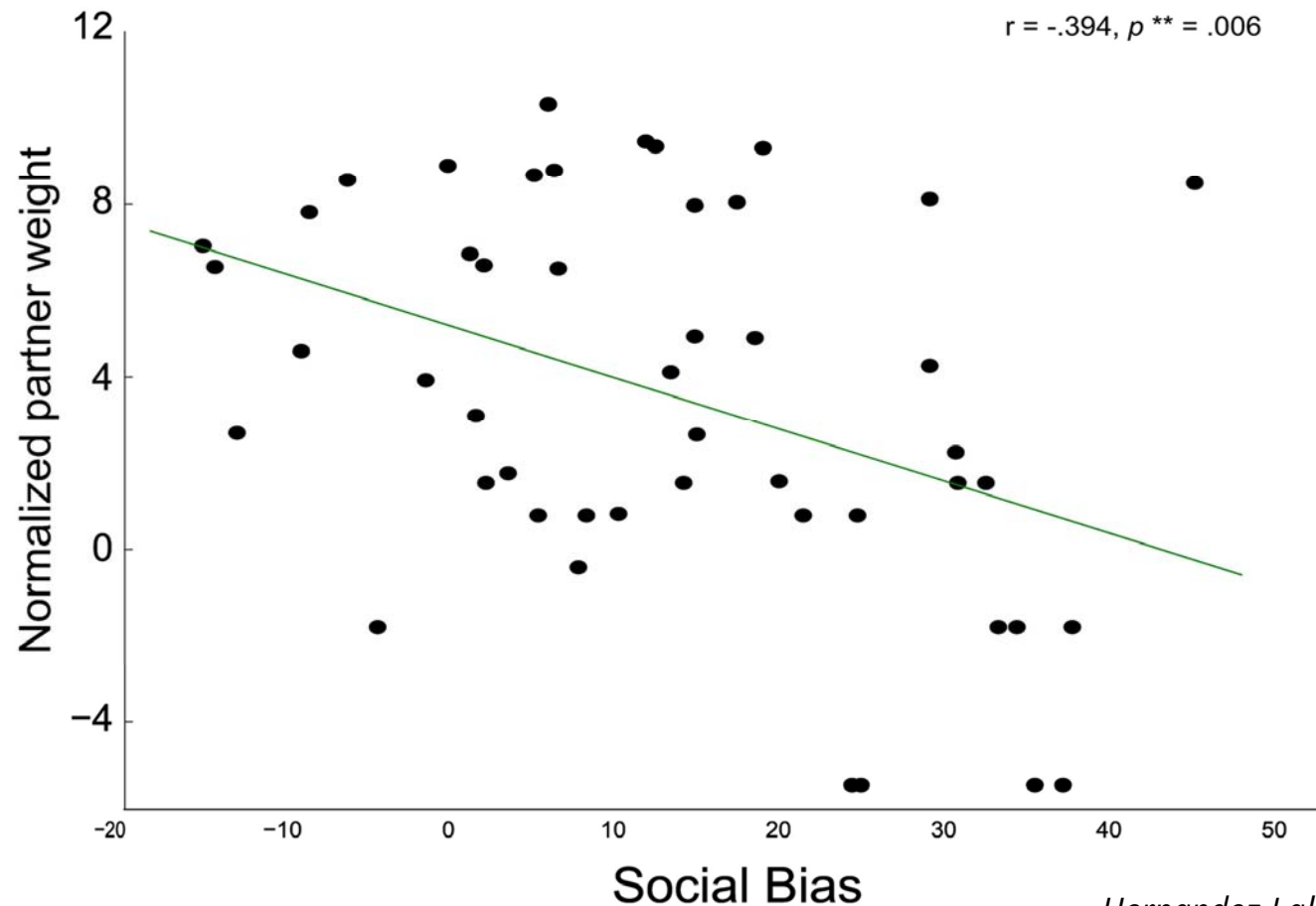
- Can be interpreted as *added social value* placed on the reward to partner



Hernandez-Lallement et al., 2015

# The Rodent Prosocial Choice Task

The heavier the actor relative to partner, the higher the social bias scores



*Hernandez-Lallement et al., 2015*

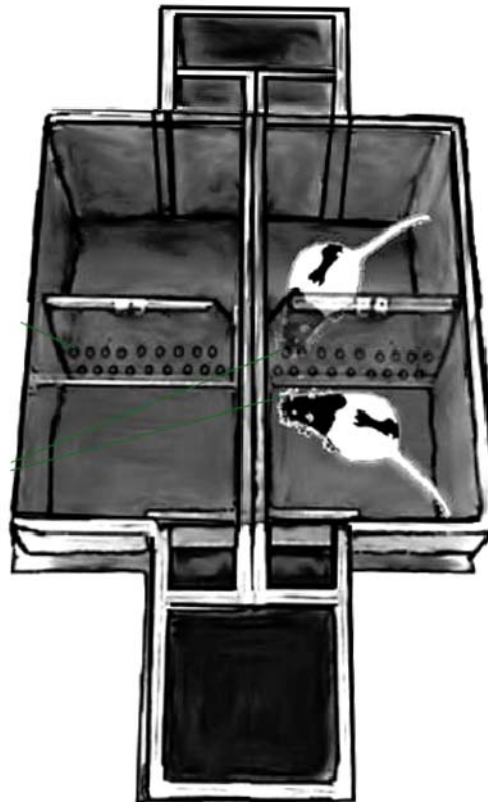


Do rats show *advantageous*  
inequity aversion?



**Do rats show *disadvantageous*  
inequity aversion?**

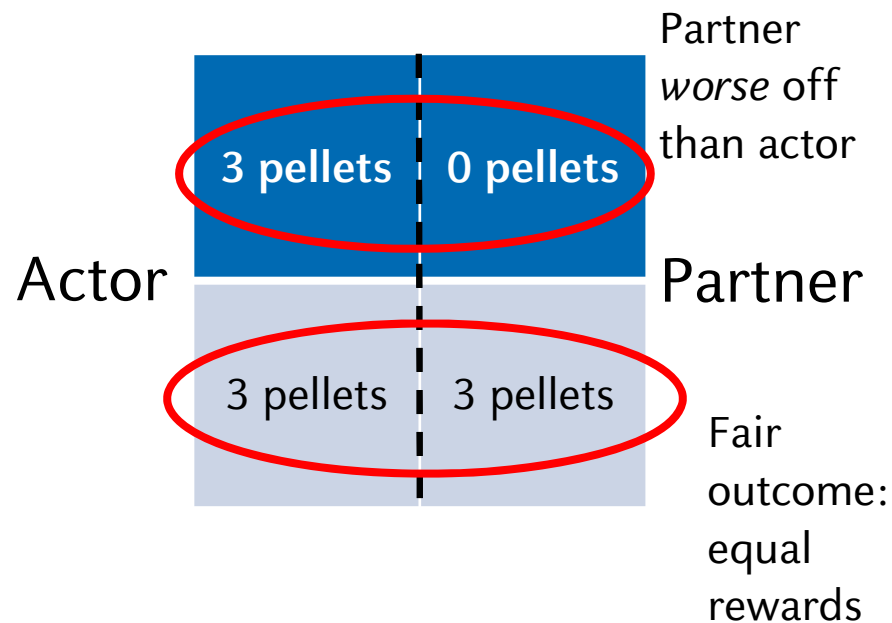
Same setup, similar task



# Disadvantageous inequity aversion

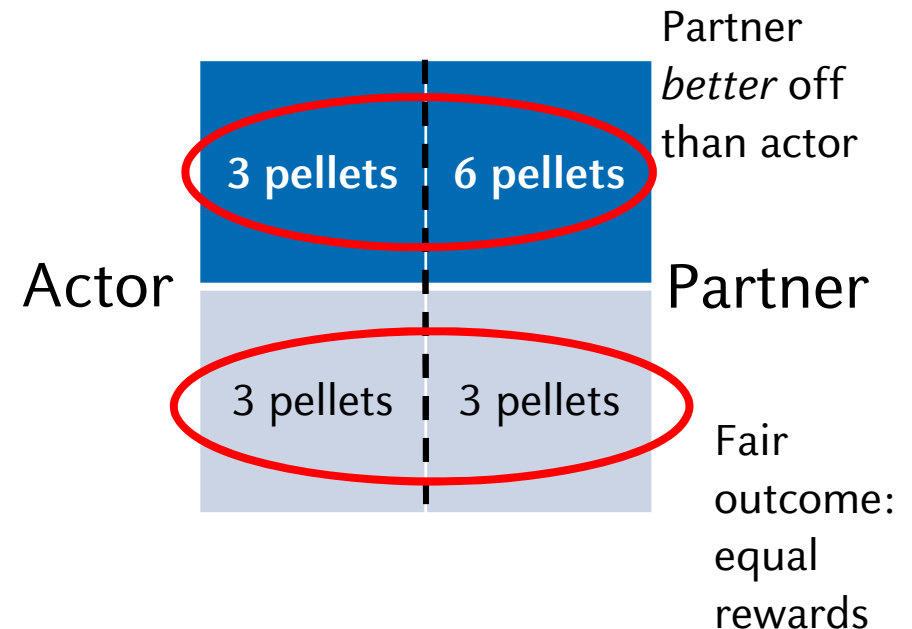
So far:

## Advantageous inequity aversion



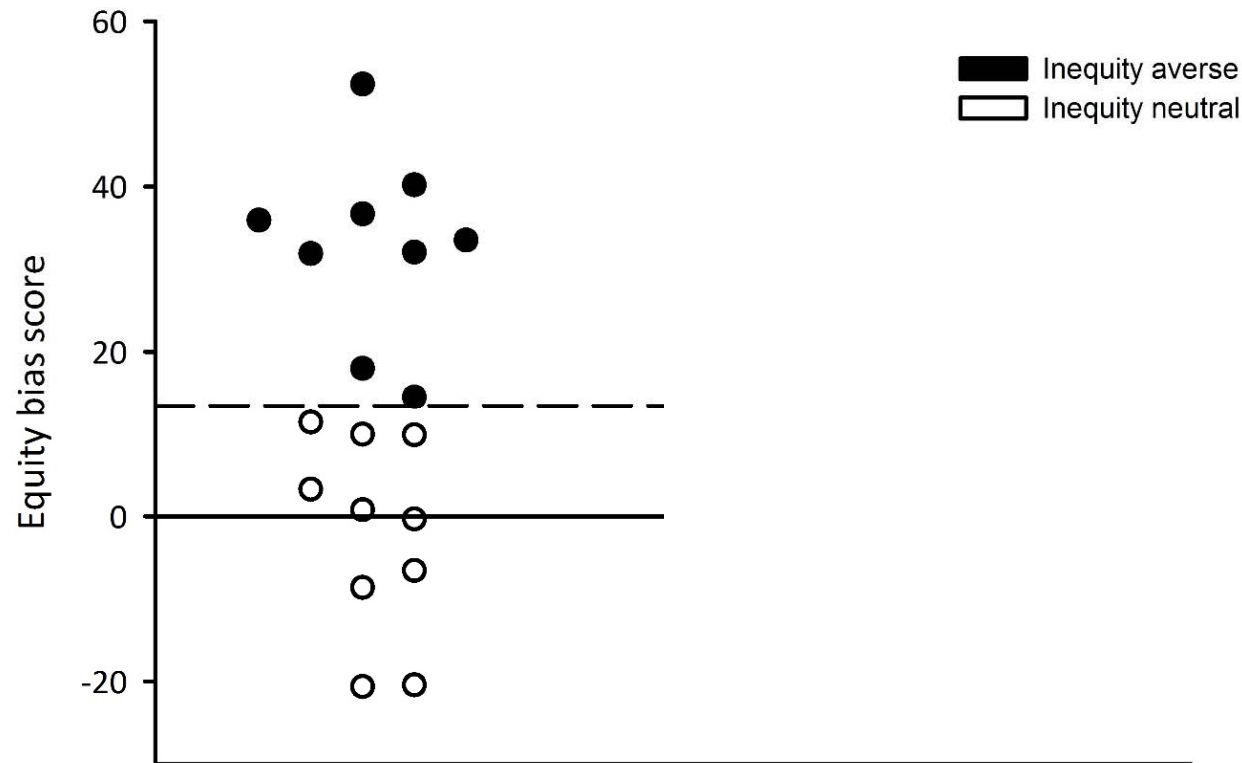
Now:

## Disadvantageous inequity aversion



*Oberließen et al., Animal Behavior, 2016*

## Rats are disadvantageous inequity averse

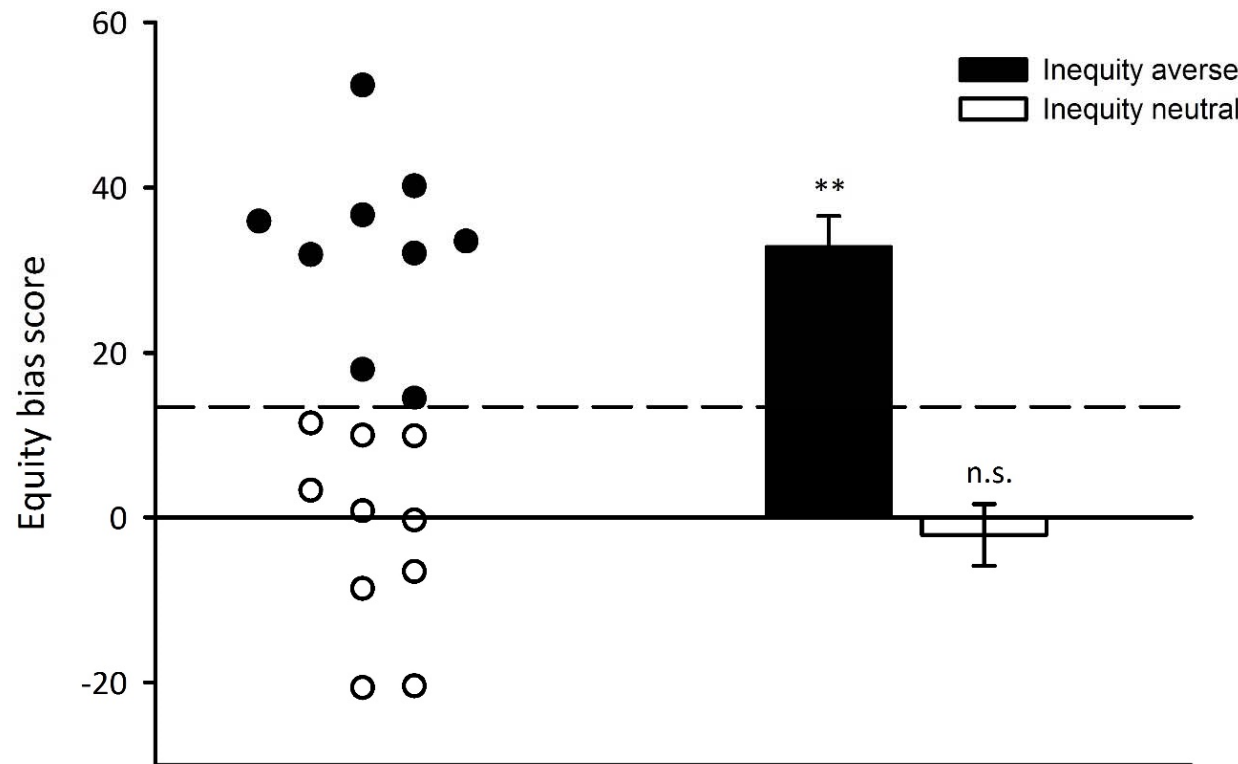


Equity bias score: Similar to social bias score, can be interpreted as measure of inequity aversion

*Oberließen et al., Animal Behavior, 2016*



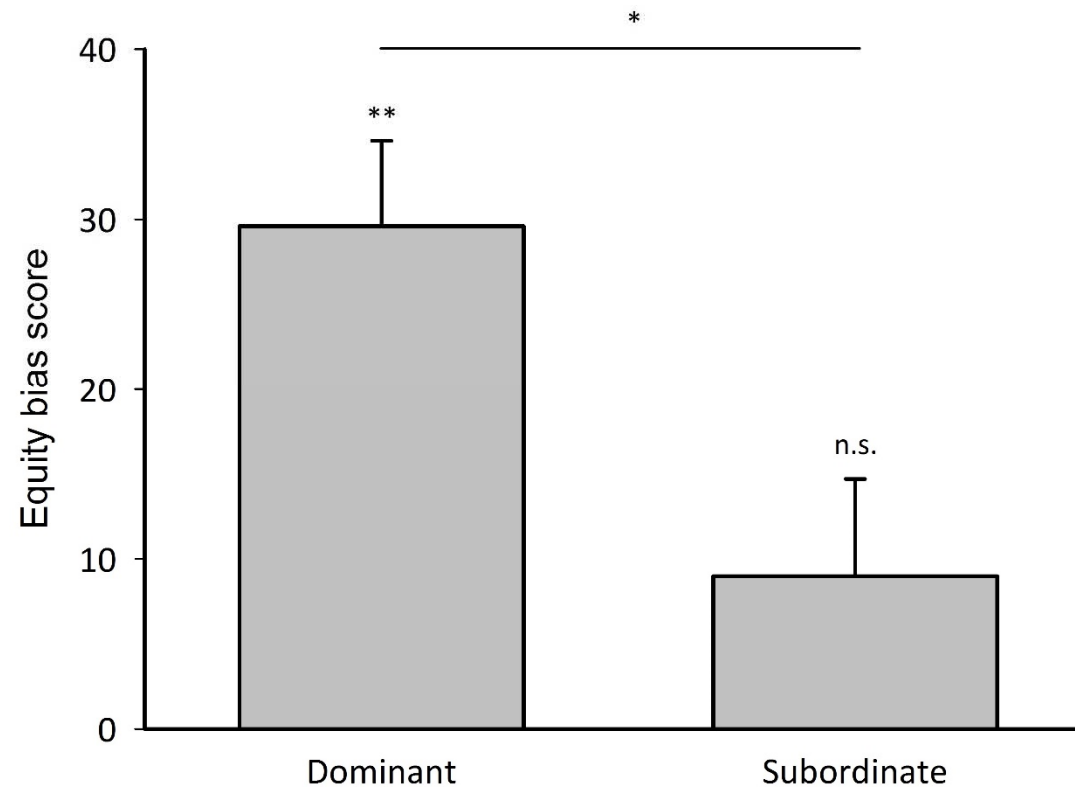
## Rats are disadvantageous inequity averse



Equity bias score: Similar to social bias score, can be interpreted as measure of inequity aversion

*Oberließen et al., Animal Behavior, 2016*

## Inequity aversion is modulated by social dominance



*Oberließen et al., Animal Behavior, 2016*

Do rats show *disadvantageous*  
inequity aversion?



# What is the neural basis of advantageous inequity aversion?



## Neural basis of inequity aversion

- Which brain region is necessary for the expression of prosocial behavior?
- One possible candidate region: **amygdala**

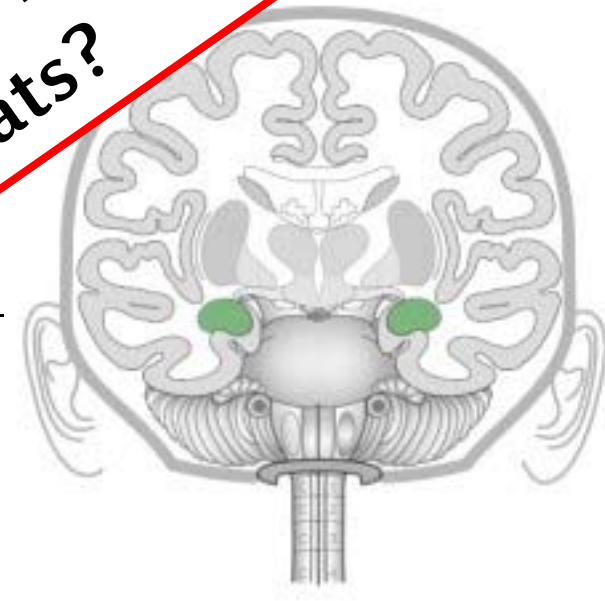




## Why amygdala?

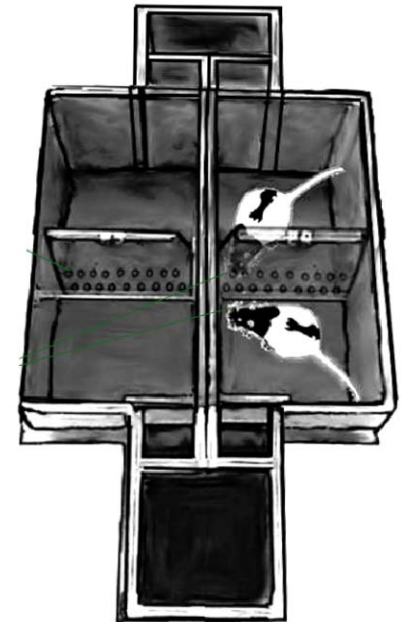
- Hypothesized to regulate...
  - ...social affiliation and avoidance (Bavel et al., 2008)
  - ...social network management (Bickart et al., 2011)
- Amygdala dysfunction is implicated in social deficits (Anderson & Kiehl, 2012)
- Primate amygdala neurons respond to social and other-rewards (Chang & Platt, 2012)
- In rodents, amygdala is involved in...
  - ...disgust (Panksepp, 1997)
  - ...transmitted food (Panksepp, 1997)
  - ...social exploration (Wang et al., 2014)
  - ...mediated social recognition (Kondo, 1992)

**What is the role of amygdala in mutual reward preferences in rats?**



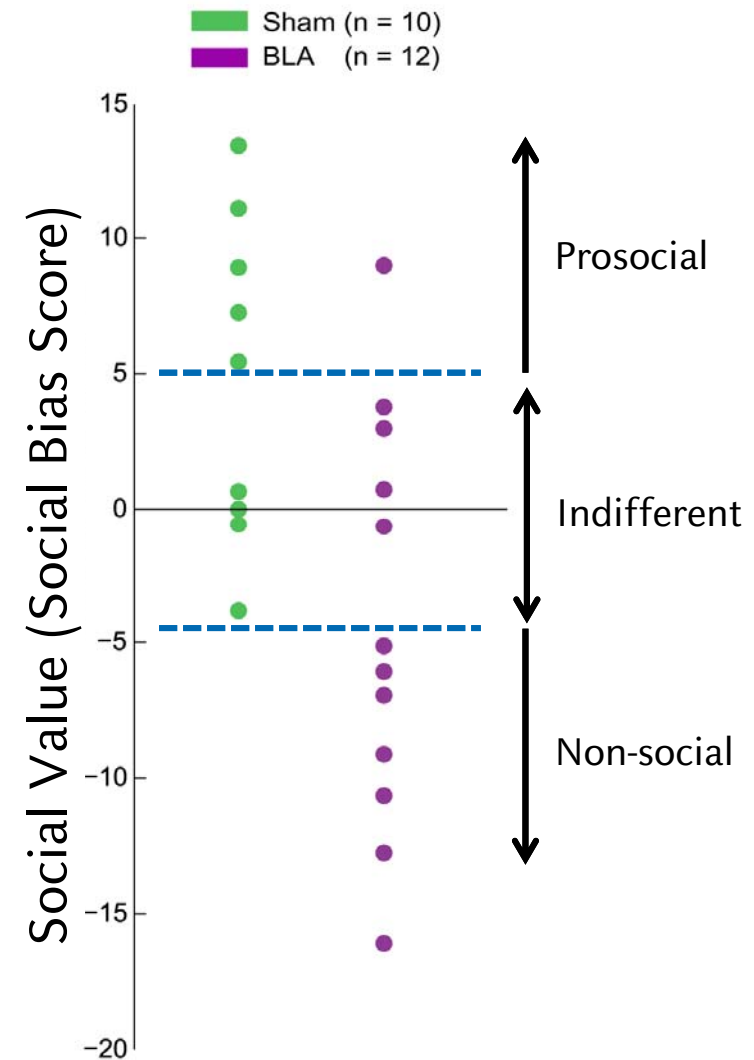
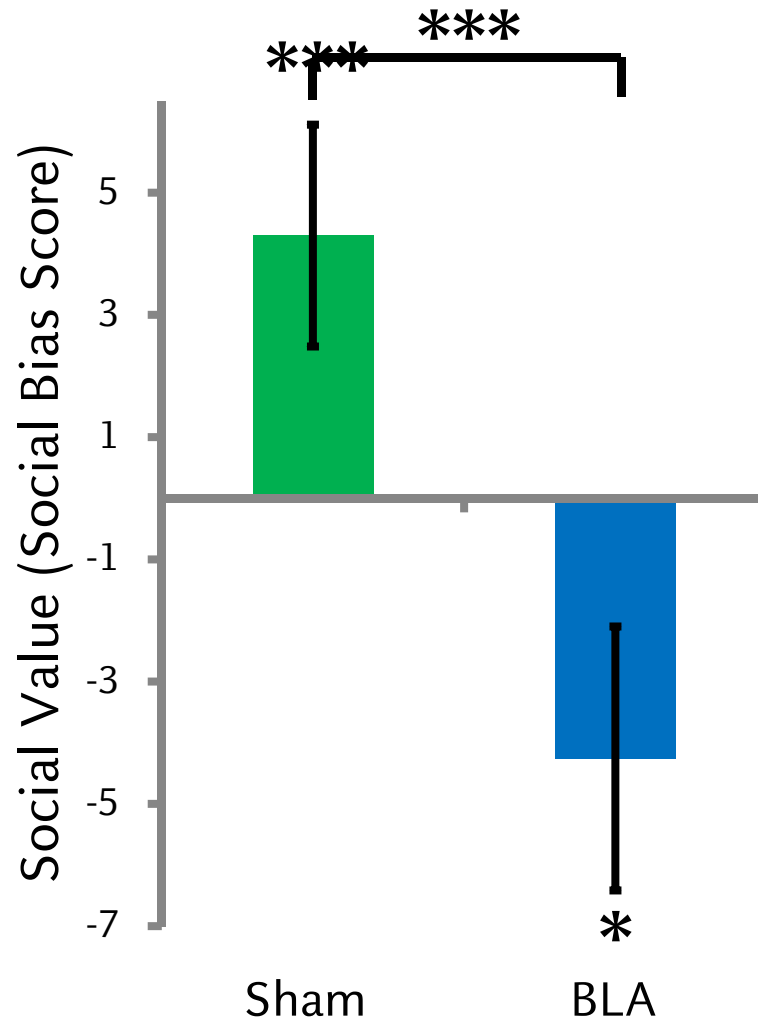
## Design

- Same prosocial choice task on advantageous inequity aversion
- Bilateral excitotoxic lesions to basolateral amygdala (BLA) or sham lesions
- Lesions done before training & testing



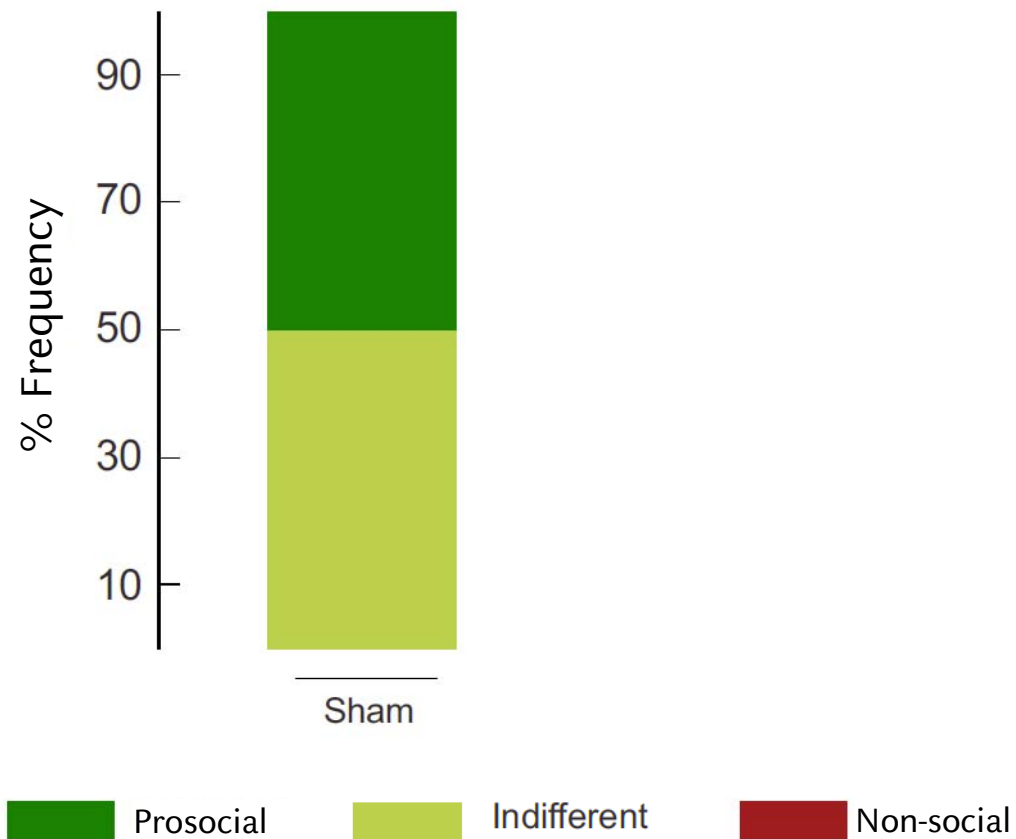
# Amygdala lesions abolish mutual reward preferences

## BLA lesion results



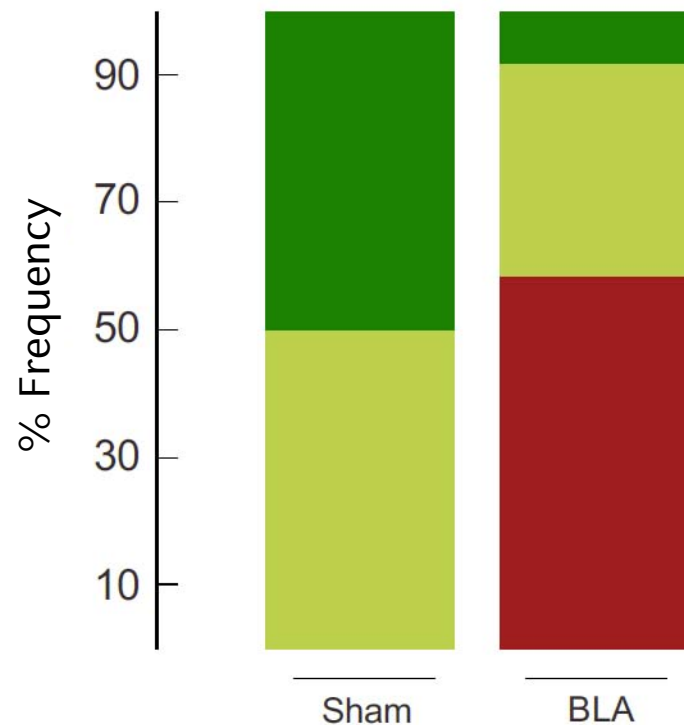
*Hernandez-Lallement et al., Neurobiol Learn Mem, 2016*

## BLA lesion results



*Hernandez-Lallement et al., Neurobiol Learn Mem, 2016*

## BLA lesion results



	Prosocial	Indifferent	Non-social
Sham	50%	50%	0%
BLA	8%	33%	59%

$p < .01$

$p < .01$

Prosocial Indifferent Non-social

*Hernandez-Lallement et al., Neurobiol Learn Mem, 2016*



**Amygdala integrity is necessary for prosocial decision making during advantageous inequity aversion**

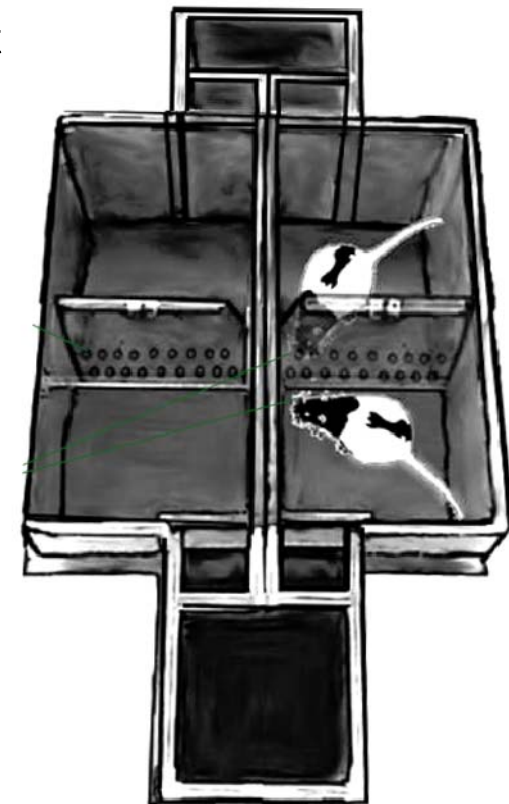


## Prosocial Behavior:

**Why do rats prefer mutual-reward outcomes?**

## Why do rats prefer mutual reward outcomes?

- Main hypothesis: *mutual-reward* preferences are the consequence of *social* reinforcement learning
- Positive social reinforcement: reward to the partner rat is associated with reinforcing social signals
  - Partner rats emit a social signal during food delivery that is rewarding for the actor rat
  - Actor rats develop preference for mutual reward alternative because it is associated with reinforcing signals emitted by the partner

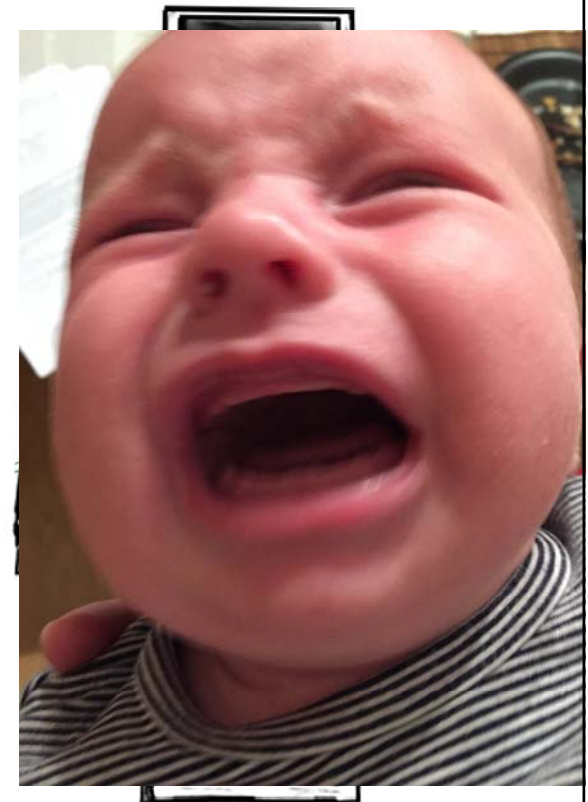


# Social reinforcement hypothesis

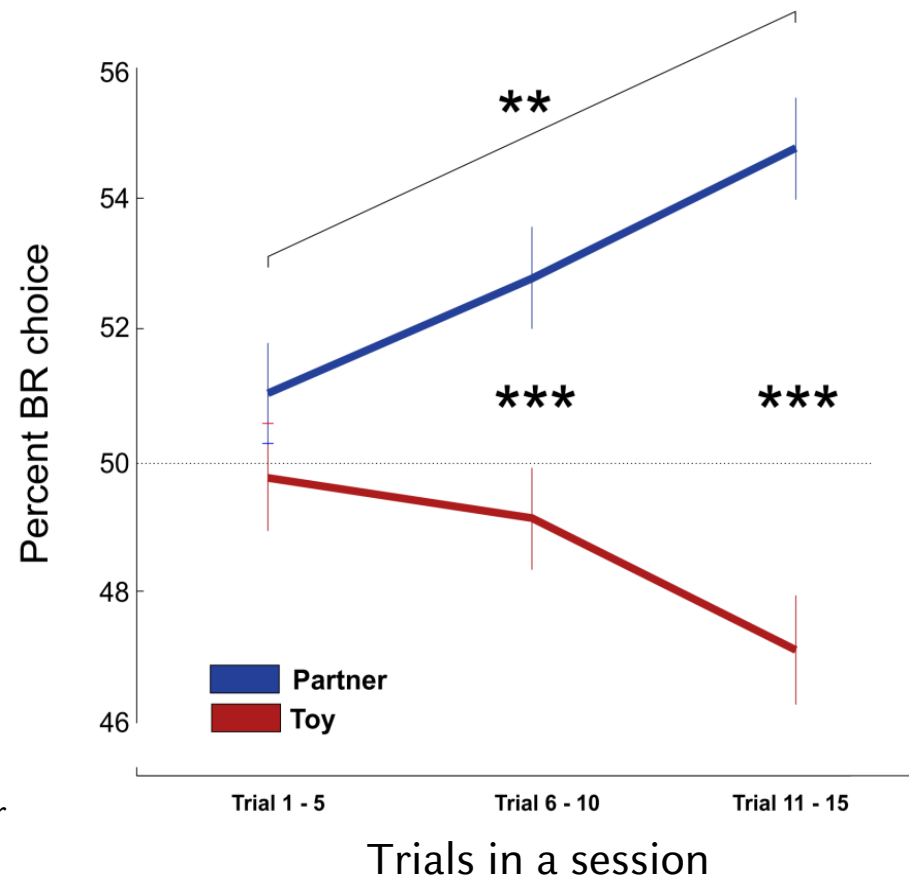


## Why do rats prefer mutual reward outcomes?

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- Negative social reinforcement: selfish choices are associated with aversive states that actor rats aim to avoid
  - Duped partner rats show „complaint“ behaviour that is possibly aversive for the actor rat



## Rats flexibly re-acquire mutual-reward outcomes after reversals

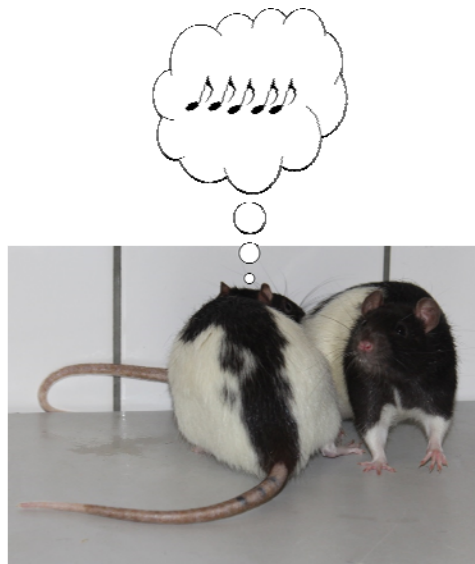


Hernandez-Lallement et al., Curr  
Topics Behav Neurosci, 2016

What is the social reinforcer?

## Hypothesis

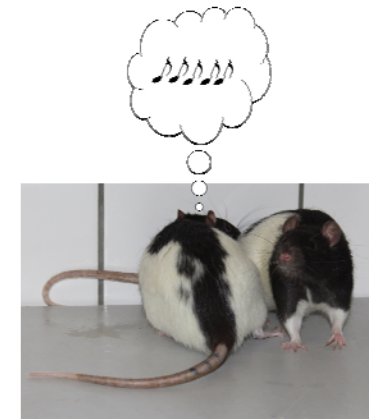
Rats' ultrasonic vocalizations (USVs) could act as social reinforcers



## Ultrasonic vocalizations in rats

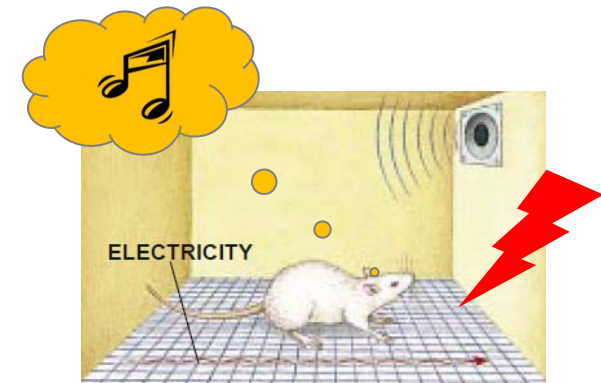
- Rats emit 50 kHz vocalizations in positive affective states („happy calls“)

- Rough-and-tumble play
- Tickling
- Ampethamine administration
- Food reward consumption



- Rats emit 22 kHz vocalizations in negative affective states („distress calls“)

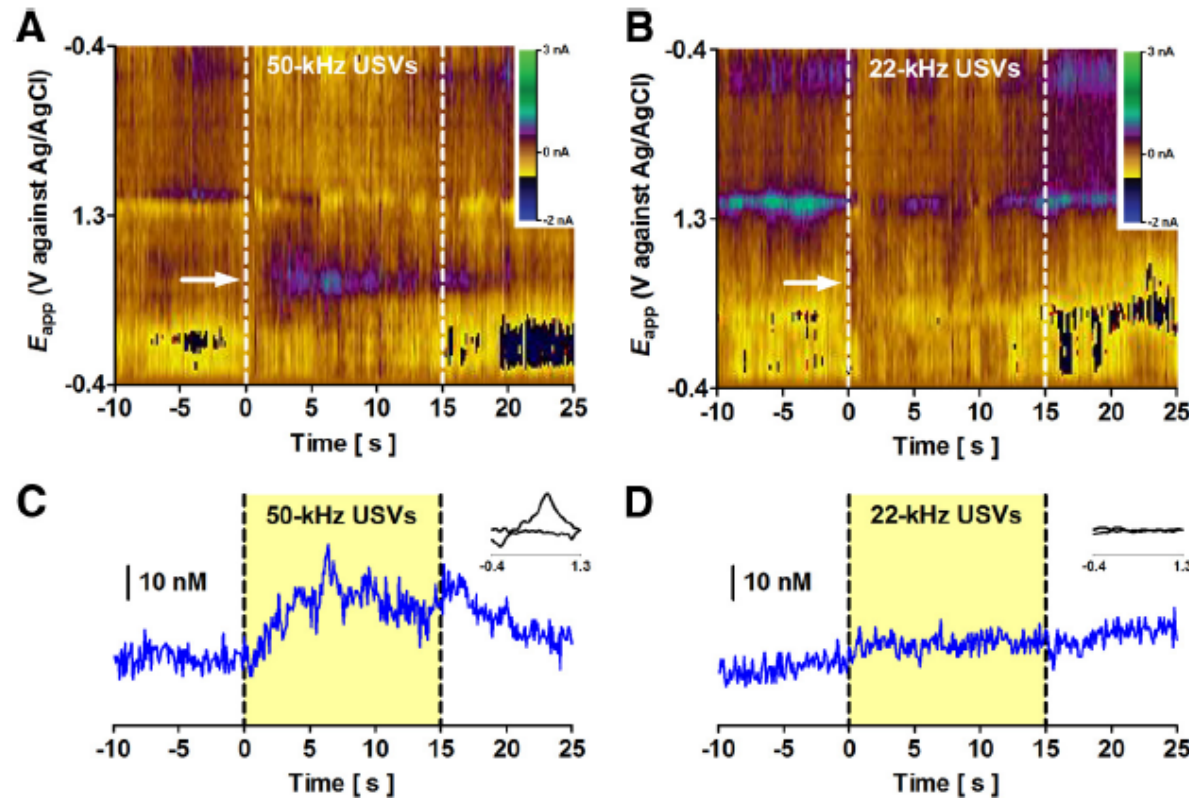
- Threatening stimuli
- Electric shocks
- Fear conditioning





## 50 kHz Vocalizations

- Listening to playback of recorded 50 kHz ultrasonic vocalizations triggers dopamine release in Ncl. accumbens



Willuhn, *J Neurosci*,  
2014

## What is the social reinforcer?

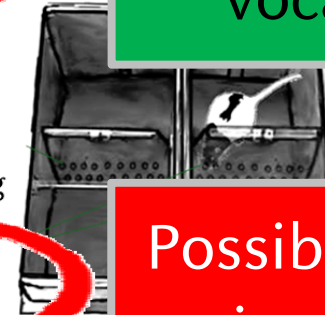
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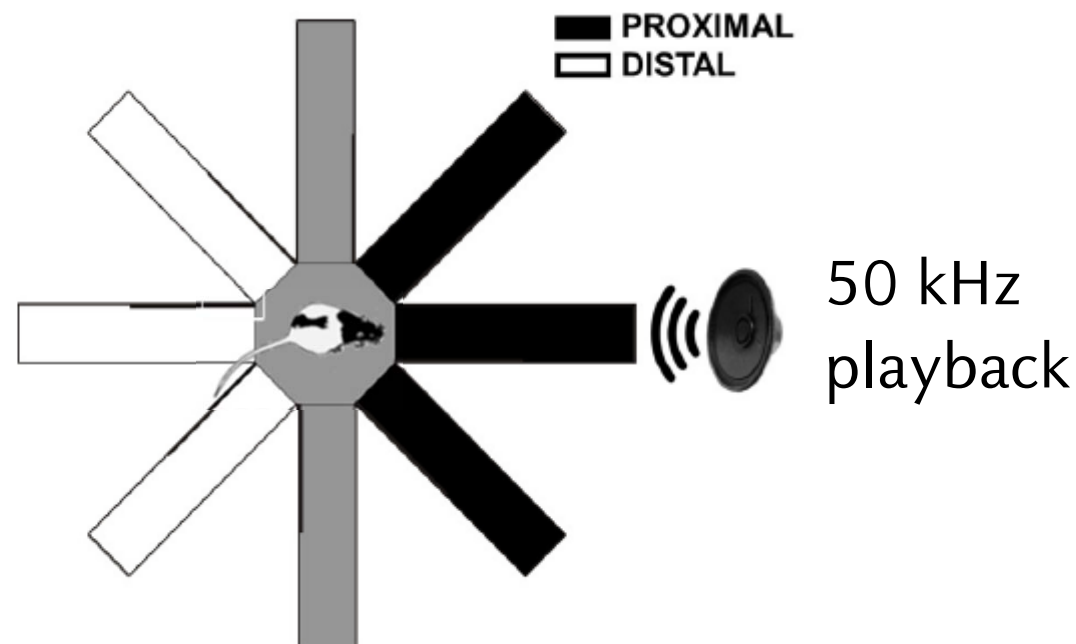
Possible candidate  
signal: 50 kHz  
vocalizations

Possible candidate  
signal: 22 kHz  
vocalizations



## 50 kHz Vocalizations

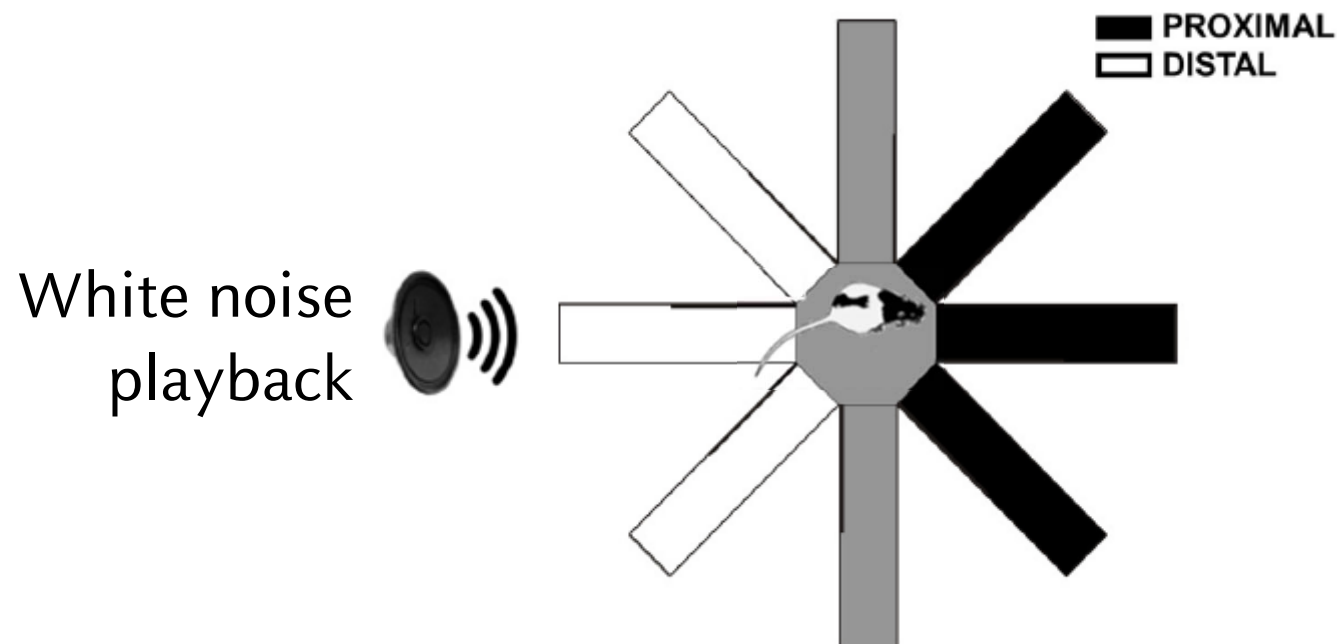
- Is it possible that listening to playback of recorded 50 kHz ultrasonic vocalizations is rewarding for a rat?



*Adapted from Seffer et al., 2014*

## 50 kHz Vocalizations

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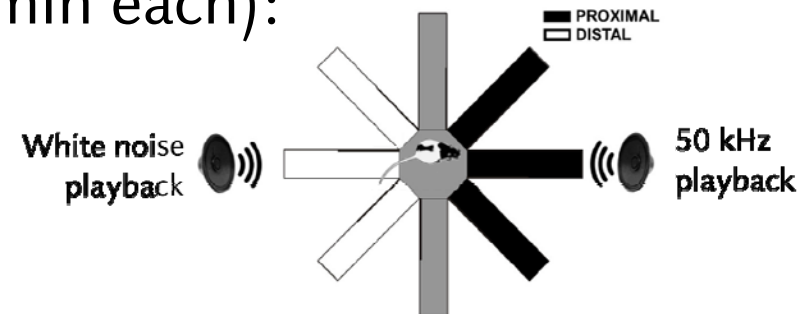
*Adapted from Seffer et al., 2014*

## 50 kHz Vocalizations

- Is it possible that listening to playback of recorded 50 kHz ultrasonic vocalizations is rewarding for a rat?

- 3 different types of playback (1 min each):

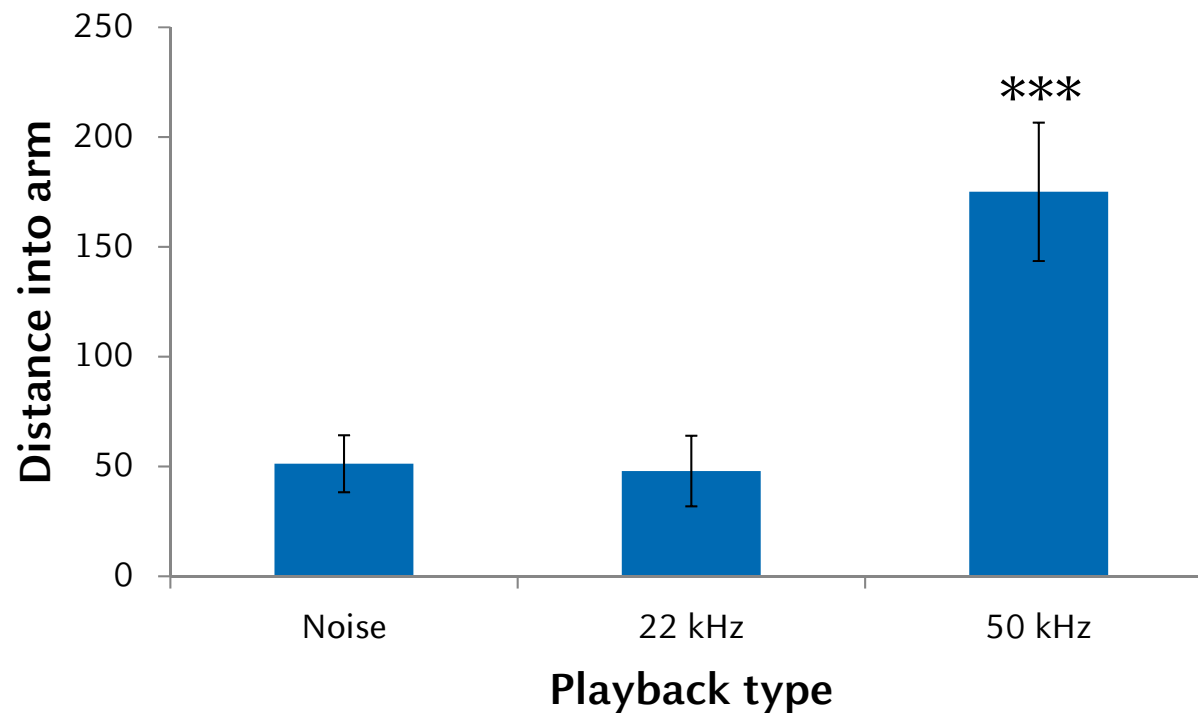
- 50 kHz USVs („happy calls“)
- 22 kHz USVs („distress calls“)
- USV white noise



- Fully randomized USV-arm associations across rats
- Fully randomized order of USV presentations
- Do rats prefer arms associated with 50 kHz playback over the other arms?

## 50 kHz Vocalizations

- Is it possible that listening to playback of recorded 50 kHz ultrasonic vocalizations is rewarding for a rat?



*Social Rodent Lab 2016*

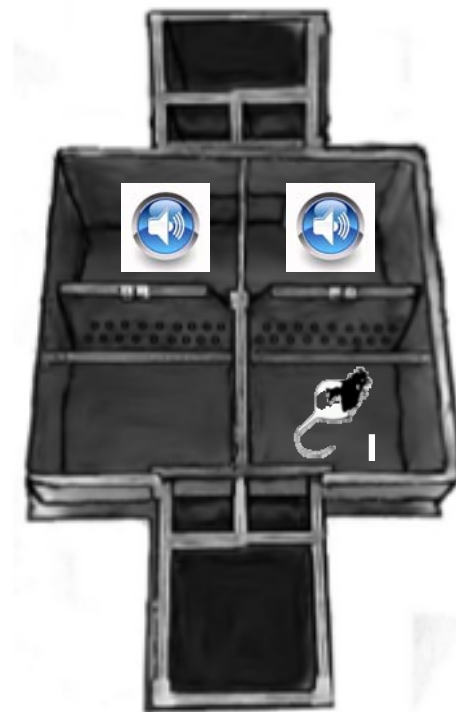
## 50 kHz Vocalizations

- 50 kHz vocalization playback triggers an orientation response
- But can this explain the preferences for the both-reward option in the Prosocial Choice Task?
- Next experiment: USVs in Prosocial Choice Task setup



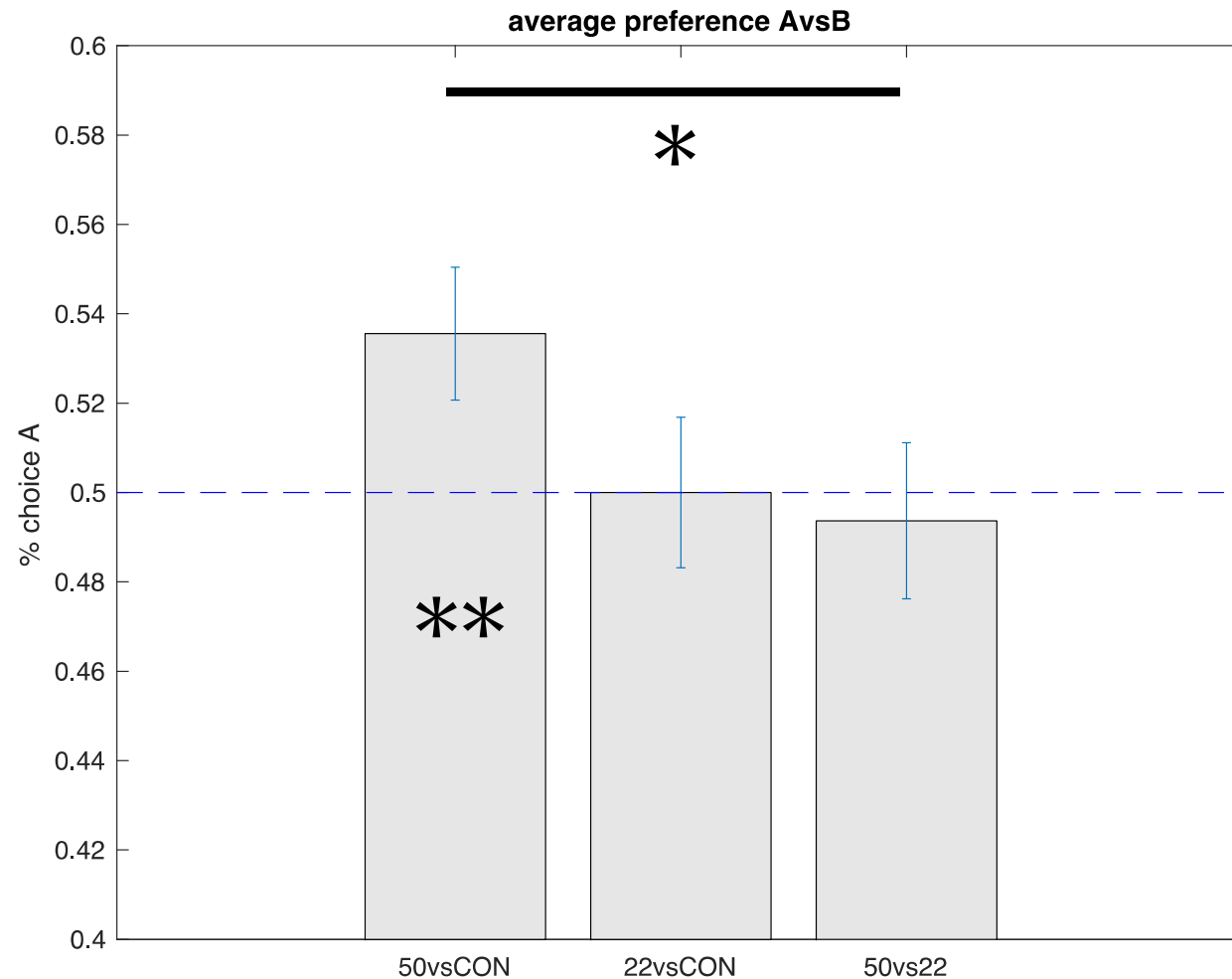
## 50 kHz Vocalizations

- No partner present
- Actor receives  $n=3$  pellets on either side
- 4 forced choice, 11 free choice
- Conditions:
  - 50 kHz vs. white noise
  - 50 kHz vs. 22 kHz
  - 22 kHz vs. white noise
- As before: frequent reversals, everything randomized etc.





## 50 kHz Vocalizations



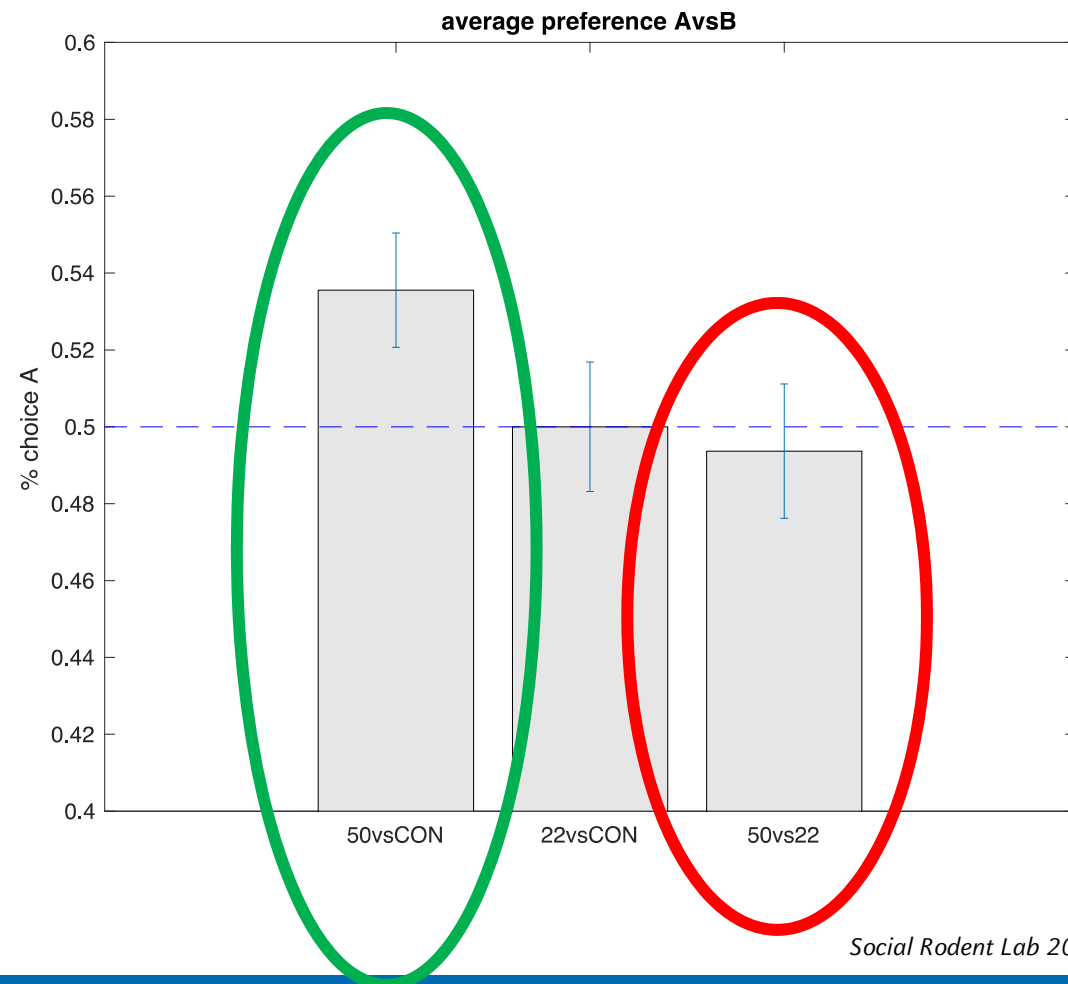
Social Rodent Lab 2016

**Positive social reinforcement:**  
50 kHz vocalizations are putative  
candidate signals



But...

- Rats prefer 50 kHz compartment over white noise compartment
- But they do not prefer 50 kHz over 22 kHz compartment
- What's with 22 kHz?
- Next experiment: record USVs during prosocial task performance
  - With real and toy partners, as usual

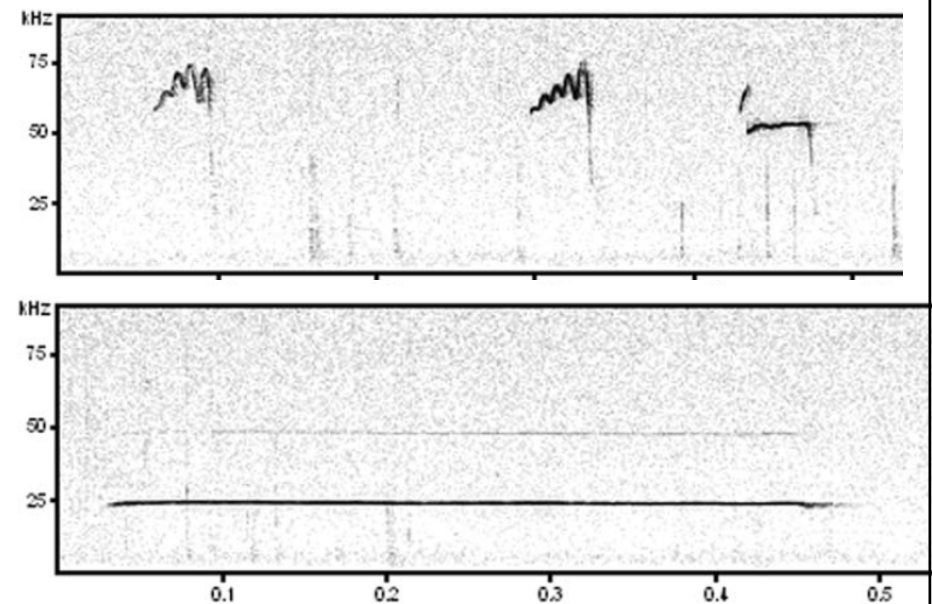


Social Rodent Lab 2016

# Social reinforcement hypothesis

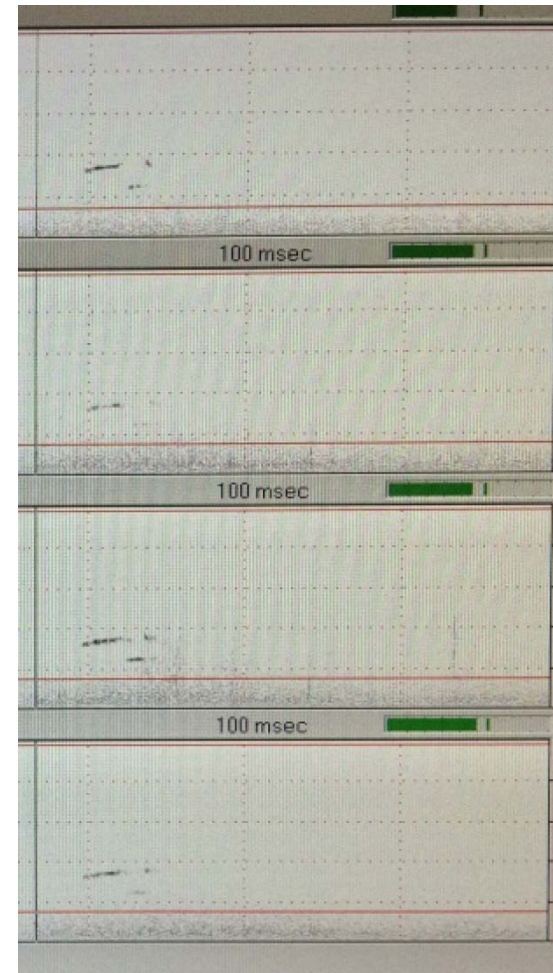


## Example USV calls as recorded



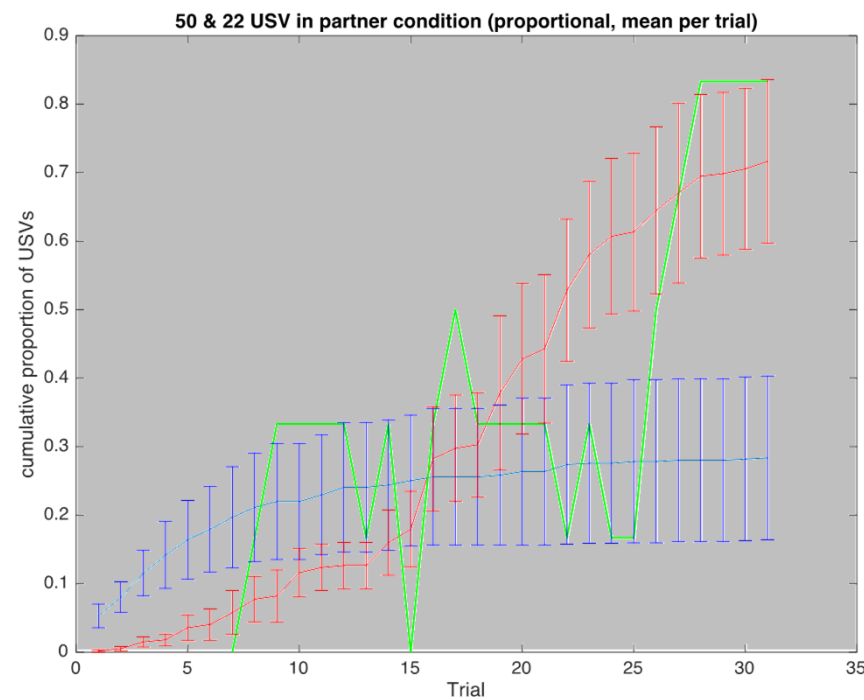
Wöhr & Schwarting 2007

# Social reinforcement hypothesis



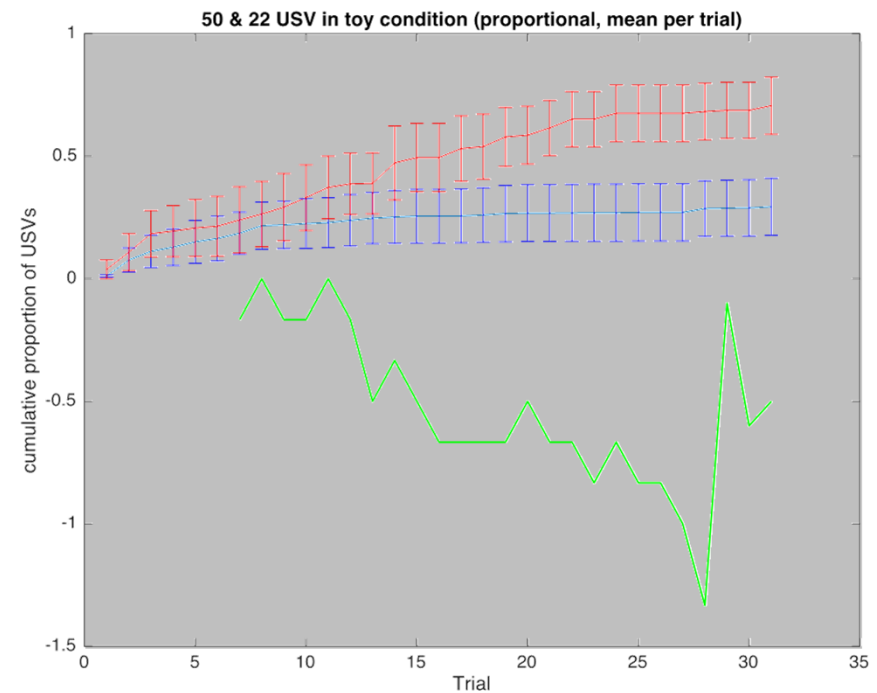
Social Rodent Lab 2016

## Partner condition



- 50 kHz („happy calls“)
- 22 kHz („distress calls“)
- % mutual reward choices (prosocial choices)

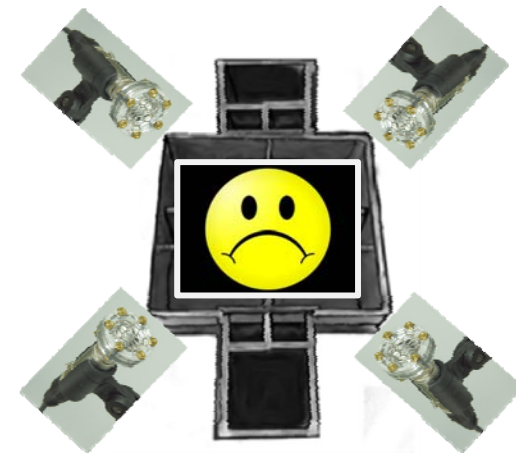
## Toy condition



*Social Rodent Lab 2016*

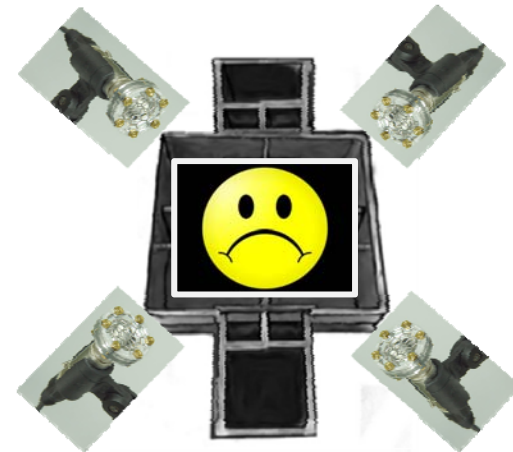
## Prosocial choices and ultrasonic vocalizations

- Here, prosocial choices did *not* correlate with 50 kHz vocalizations
- The proportion of prosocial choices increased with increasing number of 22 kHz vocalizations
- Evidence for negative social reinforcement?
- **Negative social reinforcement:  
22 kHz vocalizations are putative  
candidate signals**



## Can USV explain prosocial preferences?

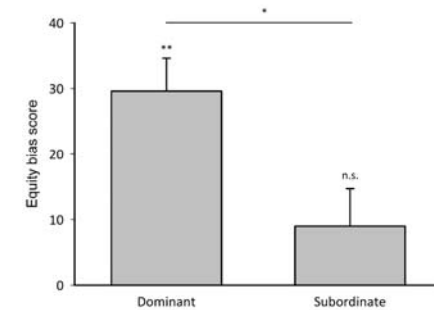
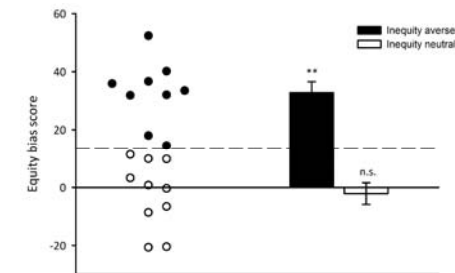
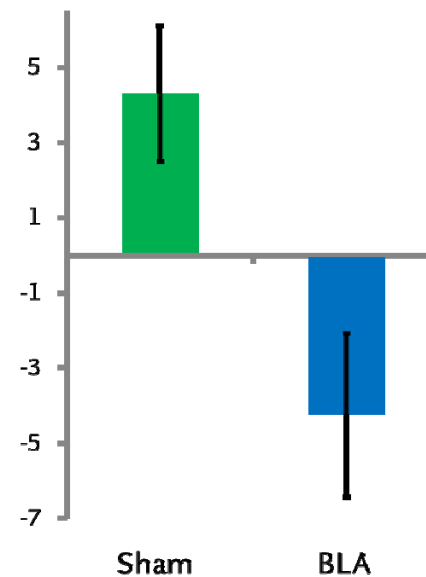
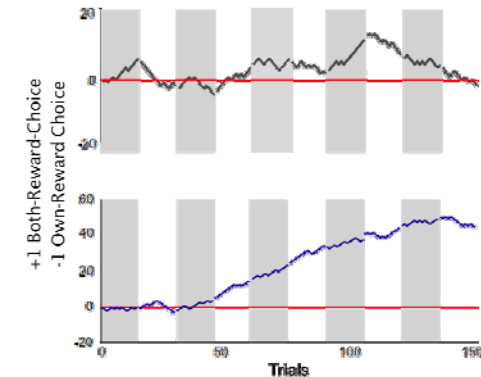
- 50 kHz vocalizations are a candidate *positive* social reinforcer for mutual-reward choices
- 22 kHz vocalizations are a candidate *negative* social reinforcer against selfish choices
- Positive and negative social reinforcement may act in concert to produce prosocial choices
- Detailed mechanisms still unknown, more research underway





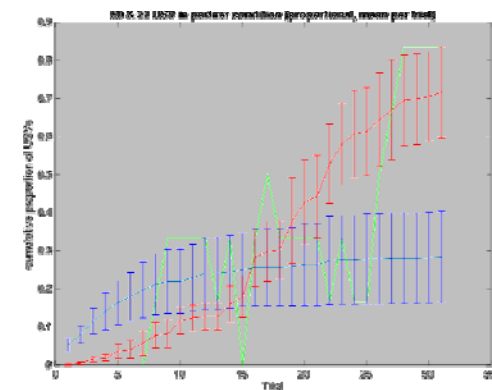
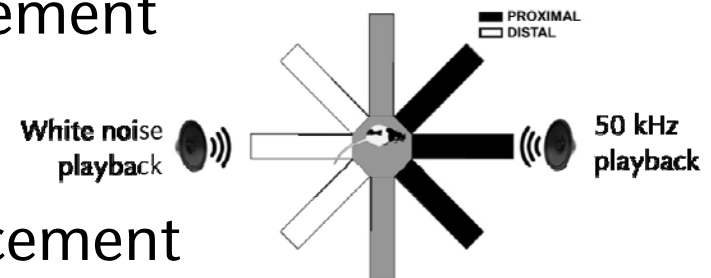
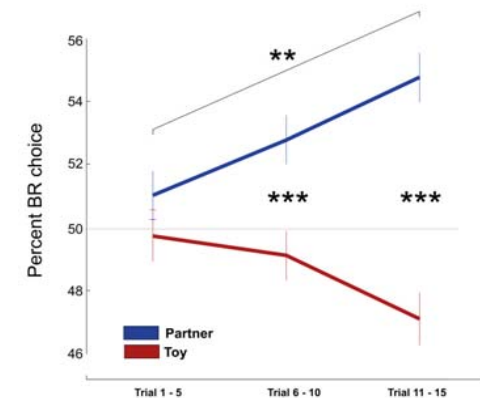
# Summary 1/2

- Rats show advantageous inequity aversion...
- ...and disadvantageous inequity aversion
- Inequity aversion is stronger in socially dominant rats
- Integrity of basolateral amygdala is necessary for the expression of mutual-reward preferences (prosocial choices)



## Summary 2/2

- Mutual-reward preferences are the consequence of social reinforcement learning
- 50 kHz vocalizations are a putative candidate for *positive* social reinforcement
- 22 kHz vocalizations are a putative candidate for *negative* social reinforcement
- Positive and negative social reinforcement may act in concert to produce prosocial behavior



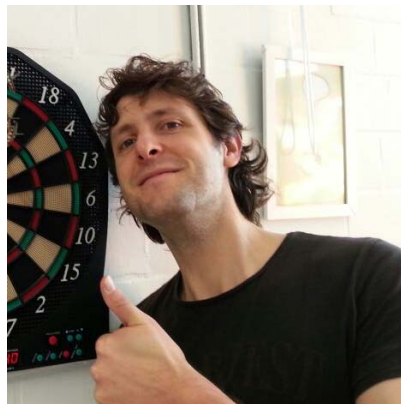
## Comparative Psychology



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Sandra Schäble



Julien Hernandez-Lallement



Lisa Schönfeld

## The Social Rodent Lab



Marijn van Wingerden



Mireille van Berkel



Sander van Gorp

**Special thanks to the  
Comparative Psychology team!**



Many thanks for your attention!

