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Review article

Towards a unified theory of emotional contagion in rodents—A meta-analysis

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ABSTRACT

Here we leverage 80 years of emotional contagion research in rodents and perform the first meta-analysis on this topic. Using 457 effect sizes, we show that, while both rats and mice are capable of emotional contagion, there are differences in how various factors modulate empathy in these species: 1) only mice show strain-specific differences in emotional contagion response; 2) although rats and mice have equivalent contagion response to familiar and unfamiliar individuals, our results show that familiarity length is negatively correlated with level of contagion in rats only; 3) prior experience with emotional stimuli almost doubles fear contagion response in rats while no changes are detected in pre-exposed mice; 4) both mice and rats tested alone show comparable reduced contagion compared to animals tested in a group; 5) emotional contagion is reduced in animals from both species missing one sensory modality compared to situations where all sensory modalities are recruited during emotional contagion. Lastly, we report similar patterns of brain activation during emotional contagion in rats and mice.

1. Introduction

In humans, witnessing the emotions of others is related to specific brain activation patterns (see (Lamm et al., 2011) for a meta-analysis). However, a range of studies demonstrate that empathy is not ubiquitous, and that a subset of the population is impaired in detecting distress in other individuals (Dolan and Fullam, 2006), showing an incongruent empathic response to other's emotions (Dawel et al., 2012; Marsh and Blair, 2008). Such individuals show deficits in the recognition of social signals (Marsch and Blair, 2008; Blair et al., 2005; Muñoz, 2009) but display intact emotional responses to unconditioned stimuli (Birbaumer et al., 2005), suggesting a social domain-specific impairment. While several theories (deficits in stimulus-reinforcement learning (Blair, 2007) or attention (Moul et al., 2012), and spontaneous vicarious perception (Meffert et al., 2013)) have been proposed to account for such social impairments, these theories have remained mostly speculative due to limited strategies for empirical testing. Indeed, while imaging techniques in humans can detect correlation links between processes, they do not enable researchers to influence neuronal activity (hence limiting causal link analysis) and have a poor spatial resolution (hence limiting accurate quantification of the neural networks involved).

Here, animal models, and rodents in particular (Panksepp and Panksepp, 2013a; Keysers and Gazzola, 2016), provide a powerful mean to put theories of empathy to the test by mapping and manipulating the neural networks involved in the perception of others' emotions (Keysers and Gazzola, 2016). Published literature on social behavior in rodents is quite extensive and ranges from the late 1940's (Anderson, 1939; Rice and Gainer, 1962; Riess, 1972; Greene, 1969; Daniel, 1942, 1943; Church, 1959; Korman and Loeb, 1961; Lavery and Foley, 1963; Baum, 1969a; Latané, 1969; Krebs, 1971) to recent influential pieces unifying the building blocks of empathy across species (Preston and De Waal, 2002; De Waal and Preston, 2017).

However, the flourishing field of animal empathy in the last decades has come with a cost, namely a wide variability in the behavioral paradigms and experimental parameters used, as well as in empathy-related definitions adopted by different studies performed in rodents (West et al., 2007; Vasconcelos et al., 2012). As a result, the published literature on this topic is often contradictive and confusing. For instance, while several recent reviews suggest that rodents should be put at the center of empathy research (Meyza et al., 2016; Keum and Shin, 2016; Sivaselvachandran et al., 2016; Panksepp and Panksepp, 2013b; Mogil, 2012), other research groups have suggested more parsimonious explanations for reported behaviors (Vasconcelos et al., 2012; Schwartz et al., 2016; Silberberg et al., 2014). A wide variety of factors (e.g. gender, relatedness between individuals, prior experience) can influence behavioral outcome measures and these are likely responsible for the

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inconsistent results in the field. It is therefore crucial to extract quantitative and qualitative data computed from a large range of studies to provide guidance for future research and assess the generalizability of behavioral essays (Gurevitch et al., 2018; Leenaars et al., 2012; Moher et al., 2015).

In this article, we leverage the large body of evidence published in the last 80 years to perform a meta-analytic review on emotional contagion in rodents. Our results provide the first rodent meta-analytic quantitative estimation of 1) emotional contagion, 2) a range of factors that influence how rodents react to other's emotions and 3) brain activation patterns during emotional contagion.

2. Methods

We followed the Preferred Reporting Items for Systematic reviews and Meta-Analyses guidelines (PRISMA, http://www.prisma-statement.org/) (Moher et al., 2015; Liberati et al., 2009; Moher et al., 2009), as well as search strategies suggested by other authors (Leenaars et al., 2012) for the screening and analysis of the relevant literature.

2.1. Information source and search strategy

This meta-analysis asked the following questions: 1) what is the effect size of emotional contagion in rats and mice and 2) what are the main factors modulating emotional contagion in these species? To identify the relevant articles, we defined emotional contagion as a behavioral response triggered by (indirect -in absence of- and direct -in presence of others-) the emotional cues of other individuals.

We used two databases to search for the relevant literature: PubMed and Web of Science. For each database, we constructed filters which included the same words (see supplementary materials, "filters"), but adapted to each database's search syntax. For both databases, a time and language filter were applied, to only include research articles published in English between 01/01/1945 and 01/01/2019. The output from each database was exported in separate tables, the tables were then combined into a single list and any duplicated article (article present in both databases) was removed from the final list of articles of interest. Each article in this combined database was reviewed to select studies that met the inclusion criteria:

(1) Article written in English language (already included in search filter, but false negatives were detected manually).
(2) Study performed on rat or mice models. We decided to limit this meta-analysis to rat and mice models because most studies were performed on these two species.
(3) Article containing original research (i.e., not review, opinions, etc…).
(4) Study reporting emotional contagion-related measures that could be extracted to measure an effect size.

As a result of our definition of emotional contagion, the screened studies featured contagion carried between a test animal (emotional recipient) and a demonstrator animal (animal that experiences an emotion and transmits it), although in some cases the emotion transfer was performed *offline* (i.e., in absence of the demonstrator, such as playback of ultrasonic vocalizations). When a study made it through to the fourth criteria, we devised a strategy to limit selection bias and to make our study selection process as objective as possible. To do so, we followed a set of rules based on the definition of emotion contagion described above, to decide whether the results reported in a screened article met the inclusion criteria. Per this definition, there were multiple points that had to be met: 1) the study measured a behavioral output originating in a rat or mice; 2) the measured behavioral output was triggered by an emotional cue originating from another conspecific (e.g., distressed foot-shocked animal); 3) the emotional cue could be direct (e.g. the presence of a stressed animal) or indirect (e.g. presentation of the urine of a stressed animal, playback of vocalizations); 4) an emotional cue could be of a positive (food intake), negative (electric foot-shock) or of neutral valence (e.g., social buffering, where the conspecific is in a neutral state and the measured subject is distressed). In a few studies ($n = 9$) where all the criteria were met, except behavioral measures could not be extracted but physiological measurements such as c-fos, corticosterone were reported, this were included in the physiology analysis.

2.2. Data coding and management

A custom coding sheet was created to extract all the relevant information with regards to animal related parameters, experimental design and risk of quantification bias. MC and JHL read and coded each selected article. To ensure that the coding was done correctly a third check was performed by PGS. Because of the large amount of data extracted from each study, we selected what we considered to be key parameters to be included and analyzed in this meta-analysis (Table 1), which encompassed potential modulators of emotional contagion, and the actual measures of emotional contagion. These dependent variables were used to compute independent effect sizes.

To ensure consistency in data extraction between all the studies, each variable described in Table 1 followed the properties described below.

Species: defined whether the study was conducted using in rats or mice.

Age: defined the age, in days, of the animals used in the study. In cases were a range was given, the average of the range provided was used.

Housing: defined the number of individuals housed together (until the first day of the experimental manipulation) with the animals from which the effect size was computed ("test animals", Fig. 1). Possible categories were: 1 single housed (animal was alone in cage), 2 (animal was housed together with another individual), 3 (animal was housed with additional two individuals) and 4 or more (animal was housed with 3 or more individuals).

Sex: defined whether the animals used were males or females. In cases where mixed-sex dyads were used, we categorized them as 'both', but due to low sample size, these studies were not included in analysis looking at sex effect.

Familiarity: defined the level of familiarity of the test animal with the animal demonstrating the emotion transferred (only in cases where the origin was another animal, and not a simple social stimuli such as USV playbacks or odors). This variable was coded as categorical and continuous. Possible categories were 1) unfamiliar pairs (animals had never encountered prior to the test), 2) familiar cagemates, 3) familiar sexual couples and 4) familiar siblings. The number of days that animals knew each other was used as the continuous value. The value for

Table 1
Encoded variables. List of study characteristics collected to investigate modulatory effects on emotional contagion.

Coded variable	Data Type	Possible Outcome
Species	Categorical	Rat, Mouse
Age	Continuous	Days of age
Housing	Categorical	1, 2, 3, 4+ animals/cage
Sex	Categorical	Male or Female
Familiarity	Categorical	Days of co-habitation/ familiar-unfamiliar
Strain	Categorical	Strain
Pre-exposure	Categorical	Yes or No
Time of Measurement relative to interaction	Continuous	Time in minutes
Emotion being Transferred	Categorical	Seeking, Aggression, Fear Lust, Care, Panic, Play (Panksepp, 2011)
Sensory modalities channeling emotional transfer	Categorical	Vision, Olfaction, Audition
Testing done in isolation	Categorical	Yes or No

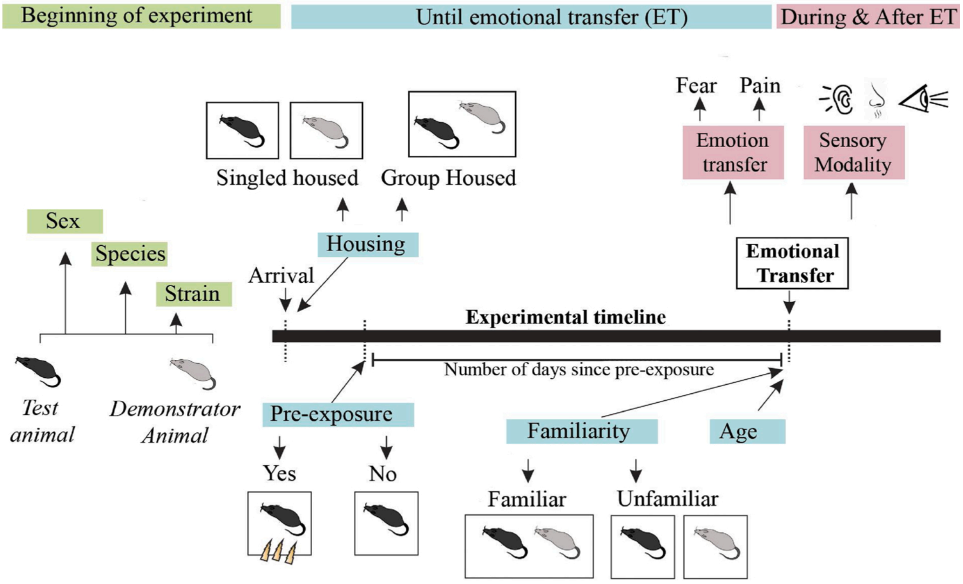


Fig. 1. Timeline of events of a typical emotional contagion experiment. The timeline depicts the variables reported for each study. Stable variables (sex, species, strain) are reported at the animal's arrival. From that point until emotional transfer occurs, a series of variables (age, familiarity and housing) are quantified. Whether pre-exposure happened before emotional transfer is also noted. During emotional transfer, variables such as emotion transferred and sensory modality channeling the transfer are reported. Finally, the dependent variable reflecting emotional contagion is reported at the time of measurement. Note that the time of measurement can happen simultaneously to emotional transfer (not depicted on figure).

unfamiliar animals was 0.

Strain: defined the strain of the animals.

Pre-exposure: defined (yes or no) whether the test animal had undergone emotional experience prior to the test. Emotional experience was defined as any prior encounter with the stimulus causing the emotional transfer during the test.

Time of measurement (relative to interaction): defined the delay, in minutes, between the interaction of animals (i.e., emotional transfer) and measurements of dependent variables. For experiments featuring a direct emotional transfer (e.g. observers witnessing the pain or fear of others), a delay of 0 min was used. When the test animal was measured alone after witnessing the emotions of others, the delay was reported in minutes.

Emotion transferred: the emotion transferred was categorized according to the nomenclature proposed by (Panksepp, 2011). Of the seven categories proposed by (Panksepp, 2011), only four were used in the emotional contagion literature: seeking, aggression, fear/anxiety and pain/panic. Seeking was selected as transferred emotion when the witnessed animal initiated approach behavior towards the source of the emotion. Aggression was selected when the witnessed animal initiated an aggressive behavior towards the source of the emotion. Fear and anxiety were selected when the witness animal displayed typical affective states such as freezing or defecating. Finally, pain and panic were selected when the witness animal showed typical pain-related behavior, such as writhing or mechanical pain.

Sensory modality during emotional transfer: defined which sensory modality or combination of sensory modalities were used during emotion transfer: vision, olfaction and/or audition. Generally, the essential contribution of a sensory modality was tested by either removing it from the emotional contagion test by using experimental constrains, such as adding an opaque partition (blocked vision) or chemically induced manipulations (e.g., $ZnSO_4$-induced anosmia) or by only using the sensory modality of interest (e.g., USV playback, urine-soaked cotton bolls or pictures)

Testing being done in isolation: defined whether (yes or no) the animal was tested alone or together with another individual.

In addition to these study characteristics, we assessed the quality and the risks of each screened article. For each study, we indicated whether 1) blinding, 2) randomization, 3) prior calculation of required sample size and 4) declaration of conflict of interest was included in the article (Table 2).

Table 2
Risk of Bias Quantification.

Encoded characteristic	Description
Blinding	Blinding was considered present when the experimenter was blinded to the experimental conditions during the analysis
Randomization	Randomization was counted as present when it was used as a procedure at any point during the study and assumed missing otherwise.
Sample Size Calculation	Sample size calculation was counted when explicitly said mentioned in the text and assumed missing otherwise.
Conflict of Interest Statement	No conflict of interest was reported when explicitly stated in the article.

2.3. Extraction of data of interest and computation of effect sizes

While statistics were reported in most studies, the comparisons often did not directly test emotional contagion. In such cases, descriptive statistics (typically mean and standard error of the mean) were manually extracted from graphical representation of data. Due to the lack of descriptive data in most manuscripts, manual extraction was performed in 86 % of the articles scrutinized (N = 106). Manual extraction was highly accurate, as confirmed by the high correlation between manual and software-based (WebPlotDigitizer) data extraction (8 randomly selected figures from 8 different papers were used: $r = 0.99$, $p < 0.0001$). When standard error of the mean (SEM) was provided in the graphical representation of data, we computed the standard deviation (SD) by using the following formula:

$$\mathrm{SD} = SEM* \sqrt{n} \tag{1}$$

Where n is the number of data points (e.g., number of subjects).

Data obtained from the studies were then used to compute the effect size (r). For categorical variables where group comparisons were performed, we created a convention in which we assigned a positive sign for one direction and a negative sign for the opposite direction. The distance from 0 in either direction quantified the strength of the effect reported. For each effect size computed, we assigned positive values to effect sizes that were in line with the following:

(1) Witnessing negative emotions in others increases fear-related responses such as freezing and startle responses. By the same token, witnessing pain in others increases hyperalgesia, i.e.,

decreases pain-related measures such as mechanical thresholds (pressure tests), paw withdrawal latencies (thermic tests) and other pain measures.

(2) Being put in presence of another individual in a neutral affective states (social buffering) decreases fear and anxiety responses.

(3) Witnessing positive emotions in others increases seeking-related behavior, such as locomotion and approach behavior.

(4) Witnessing emotions of a familiar individual triggers higher emotional contagion than for unfamiliar individuals.

(5) Females show higher emotional contagion than males.

(6) Pre-exposed animals show higher emotional contagion response compared to non-pre-exposed ones.

(7) Group-housed animals show increased emotional contagion in comparison with single-housed ones.

(8) Animals presented with an emotional stimulus that triggered all their sensory modalities (i.e., audition, olfaction and vision) show stronger emotional contagion response compared to animals presented with an emotional stimulus recruiting a subset of these modalities (e.g., blinded by an opaque partition) or only one of these sensory modalities (e.g., smell of a fear conditioned animal)

In this meta-analysis, effect sizes were calculated as a standardized mean difference (ES; (Lipsey and Wilson, 2001; Leichsenring, 2001)). When comparisons used two independent groups (i.e., between-subjects comparison, typically experimental *vs* control), we used the following computation for calculating the effect size:

$$ES = \frac{M_1 - M_2}{\sqrt{\frac{\left[\left(SD_1^2 * n_1\right) + \left(SD_2^2 * n_2\right)\right]}{(n_1 + n_2)}}} \tag{2}$$

where M, SD and n represent the mean, standard deviation and sample size for experimental and control group 1 and 2, respectively.

When comparisons used two measures from the same group (i.e., within-subjects comparison, typically baseline *vs* test time point), we used the following computation for calculating the effect size:

$$ES = \frac{M_{(t+i)} - M_t}{\sqrt{SD_{(t+i)}^2 + SD_t^2}} \tag{3}$$

where M_t is the mean initial measurement (usually baseline), $M_{(t+i)}$ is the measurement at a second time point, SD_t is the standard deviation of the distribution during the initial measurement, $SD_{(t+i)}$ is the standard deviation of the distribution at the second measurement point, and N represents the sample size of the group.

In order to bring all measures to the same metric and to ease the interpretation, effect sizes were transformed into correlation coefficients (r). The effect size estimation was done using procedures thoroughly described elsewhere (Hedges and Olkin, 1985). To convert the standardized mean difference to r, the following equation was used:

$$r = \frac{ES}{\sqrt{ES^2 + 4}} \tag{4}$$

When the relevant statistics were provided in the article, effect sizes were computed using the adequate formula:

$$r = \frac{t^2}{\sqrt{t^2 + df}} \tag{5}$$

where t is the *t* value, and df is the degrees of freedom.

$$r = \sqrt{\frac{F}{F + df}} \tag{6}$$

where F is the F value, and df is the degrees of freedom.

Finally, in the rare cases where no data was displayed graphically and only p-values were available, the p-values were used to determine z-scores. When p values were reported as greater or lower than alpha level (< or >; alpha typically = .05), the p-values used to determine z-score was set at p = 0.1. These studies (N = 6) were all published between 1955 and 1981.

$$r = \frac{Z}{\sqrt{N}} \tag{7}$$

where z is the z score value and N is the sample size.

2.4. *Combining effect sizes and comparisons*

Since the value of r becomes increasingly skewed as it gets further from 0, we normalized effect sizes using Fisher transformation (Hedges and Olkin, 1985), applied to r as follows:

$$z_r = 0.5 * ln\left[\frac{1 + r}{1 - r}\right] \tag{8}$$

where r is the effect size computed through the methods described above. By convention, z_r was converted back to r for ease of interpretation (Lipsey and Wilson, 2001).

In order to correct for biases caused by low sample size (< 20 or 10 in each group, see (Nakagawa and Cuthill, 2007)), we computed the unbiased z_r (z_{ru}) value using the equation proposed by (Hedges and Olkin, 1985; Nakagawa and Cuthill, 2007):

$$z_{ru} = z_r * \left[1 - \frac{3}{4 * (n_1 + n_{2)}) - 9}\right] \tag{9}$$

where n1 and n2 are sample sizes of two comparison groups, and the z_r is the biased effect size estimated in eq. 8.

2.5. *Random effect model*

When conducting meta-analytic approaches, it is necessary to use either a fixed effect or a random effects statistical model. A fixed effect model assumes that all effect sizes are estimating the same effect, whereas a random effects model accounts for differences in the between-studies effect. Since the chosen model affects the interpretation of the summary estimates, we tested which model to use by conducting a heterogeneity test that generates the Q-statistic described in eq. 14. The Q value is a measure of the dispersion of the effect sizes. This measure follows the chi square distribution with k-1 degrees of freedom, where k is the total number of effect sizes. In this meta-analysis, the Q value was highly significant ($\chi^2_{(350)} = 954.63$, $p < 0.001$), supporting the use of a random effects model. This model assumes that the variance of each effect size (v_i, eq. 10) is composed of variance due to intrinsic sampling errors (v_o, eq. 11 & 12) plus other sources of randomly distributed variability (v_r, eq 12). To estimate these values, we used formulas 10 through 15 thoroughly described by (Lipsey and Wilson, 2001; Nakagawa and Cuthill, 2007):

$$v_i = v_0 + v_r \tag{10}$$

$$v_o = SE^2 \tag{11}$$

$$SE = \frac{1}{\sqrt{n - 3}} \tag{12}$$

$$v_r = \frac{Q - (k - 1)}{\sum w_i - \left(\sum w_i^2 / \sum w_i\right)} \tag{13}$$

$$Q = \sum w_i Zru_i^2 - \frac{\left(\sum w_i Zru_i\right)^2}{\sum w_i} \tag{14}$$

$$w_i = \frac{1}{SE^2} \tag{15}$$

To complement the Q statistic, we also calculated I^2 statistic using Eq. 16, which measures the percent of variance between studies which is due to true heterogeneity rather than chance (Higgins and Thompson, 2002; Higgins et al., 2003):

$$I^2 = \frac{Q - df}{Q} \tag{16}$$

where Q is calculated using Eq. 14 and df is the number of effect sizes minus one, with higher percent values indicating higher heterogeneity. For this meta-analysis, the $I^2 = 63.3$ %, $p < 0.001$, indicating substantial amount of heterogeneity and giving further support for a random model analysis.

For each variable and its different levels, we calculated the mean effect size, 95 % confidence intervals (CI) and z score value using Eqs. 16–19.

$$\overline{Z}_{ru} = \frac{\sum w_i z_{rui}}{\sum w_i} \tag{17}$$

$$95\%\ CI = \overline{Z_{ru}} \pm 1.96(SE_{\overline{z}_{ru}}) \tag{18}$$

$$SE_{\overline{z}_{ru}} = \sqrt{\frac{1}{\sum w_i}} \tag{19}$$

$$z = \frac{\overline{Z}_{ru}}{SE_{\overline{z}_{ru}}} \tag{20}$$

2.6. Physiology data: corticosterone and c-fos

In addition to behavioral data, we extracted corticosterone levels (17 studies) and c-fos activation patterns (16 studies) from a subset of studies. For c-fos analysis, no meta-analytics procedures could be performed for some structures given the low number of effect sizes associated with these brain areas (see results). Effect sizes were extracted and analyzed using Python, and color coded effect sizes were overlapped on the rat brain atlas (Paxinos and Watson, 1998), and the Allen mouse brain atlas (https://mouse.brain-map.org/static/atlas). All effect sizes in the corticosterone and c-fos dataset were subjected to the same transformations and benchmarking as behavioral effect sizes.

2.7. General analysis

It is worthwhile noting that some studies used the same animals to measure emotional contagion and the effect of a given modulator on emotional contagion, and thus resulted in 2 non-independent effect sizes extracted from the same group of animals (N = 23 studies). For these scenarios, the relevant effect size was used for either analysis of emotional contagion or modulator effect. However, since we present separate analysis for emotional contagion and modulators of emotional contagion (see results), the effect sizes used in each analysis remain independent. Moreover, because of consistent differences in the paradigms and measurements used between rats and mice, as an *a priori* decision, all the analysis conducted were performed separately for rats and mice.

For statistical comparison of the levels within modulators we used the meta-analysis module of JASP (JASP Team 2019, Version 0.10.2) and ran a random effects model (restricted ML). Given that for some modulators (i.e., familiarity, memory, sex, sensory modality) there were studies that conducted experiments to specifically test the role of a given modulator, we used these studies to run an additional separate analysis where we only include studies doing this type of analysis (e.g., studies that only looked at familiarity effect).

To assess publication bias, asymmetry in a funnel plot showing study precision (1/standard error) against observed effect sizes was tested using a non-parametric rank test. Also, to estimate the number studies with an average null result needed to bring the significance of the meta-analysis to a significant level of $\alpha = 0.05$, a fail-safe N was estimated (i.e., file drawer analysis). Both the funnel plot and fail-safe N tests were conducted using JASP 0.10.2.0.

3. Results

3.1. Main findings

An exhaustive search (Fig. 2A) of the rodent emotional contagion literature yielded a final count of 124 studies, 457 studies measuring behavior and 174 effect sizes measuring physiological markers. (Table 3). From the 457 behavioral effect sizes, a subset (N = 350) directly measured emotional contagion and 107 effect sizes examined modulators of emotional contagion (e.g., familiarity) (Fig. 2F).

Quality control check of all the studies showed a suboptimal number of papers reporting blinding (45 %) and randomization (61 %) procedures and only 4% of studies reporting sample size calculations (Fig. 2B). Noticeably, no study reported any conflict of interest.

Each paper was scrutinized to identify experimental details related to emotional contagion processes. The literature on emotional contagion, which has witnessed a drastic surge in number in the last decades (Fig. 2C), is quite heterogeneous in types and nature of experimental manipulations. Typically, studies on rodent emotional contagion featured an individual experiencing a specific emotional state while another individual witnessed the emotional display (Atsak et al., 2011b). Although, the emotional display was generally produced by a conspecific, in some cases only odors (Kiyokawa et al., 2009), auditive (Wöhr and Schwarting, 2007) or visual cues (Nakashima et al., 2015) from other emotionally-stimulated conspecifics were presented to the witness.

We also identified a wide range of dependent variables reported as proxy measures of emotional contagion. Overall, most effect sizes (54 %) used freezing as a dependent variable (Fig. 2D), believed to reflect anxiety and fearful states in rodents. Among the remaining effect sizes, more than a fourth (27 %) used pain-related dependent variables, typically paw withdrawal latencies, mechanical pain threshold, writhing and tail pinch tests. The remaining effect sizes (18 %) used other, diverse dependent variables, such as defecation rate, latency to move or licking behavior.

For each effect size computed, we characterized the type of emotion that was transferred to the measured animal and thus elicited the emotional contagion response. We followed the classification of emotions proposed by (Panksepp, 2011) (Fig. 2E) which distinguished between positive (care, lust and play) and negative emotions (aggression, pain/panic and fear/anxiety). Using this classification, we found a profound lack of studies investigating emotional contagion of positive emotions. Among these, no studies were found to use lust or care emotional categories. A subset of studies used emotional stimuli classified as seeking (n = 28), which represented studies that measured approach to stimuli (i.e., seeking) conveying emotional information (typically an approach to ultrasonic vocalizations playback, see (Wöhr and Schwarting, 2007)). Most experiments investigated emotional contagion using negative emotions (fear/anxiety: n = 293, pain: n = 134, aggression: n = 2). Within the negative emotion category, 64 % of total studies used freezing as a dependent variable (fear/anxiety) and 29 % used pain-related measures (Fig. 2E). For the negative emotions, we clustered studies into three pools: 1) fear/anxiety, 2) pain and 3) other category, which included studies that used a variety of dependent variables. This ensured that the analysis of fear and pain emotions was based on similar dependent variables. Overall, because of the substantially larger number of studies investigating fear and pain, we focused on these two categories in this meta-analysis.

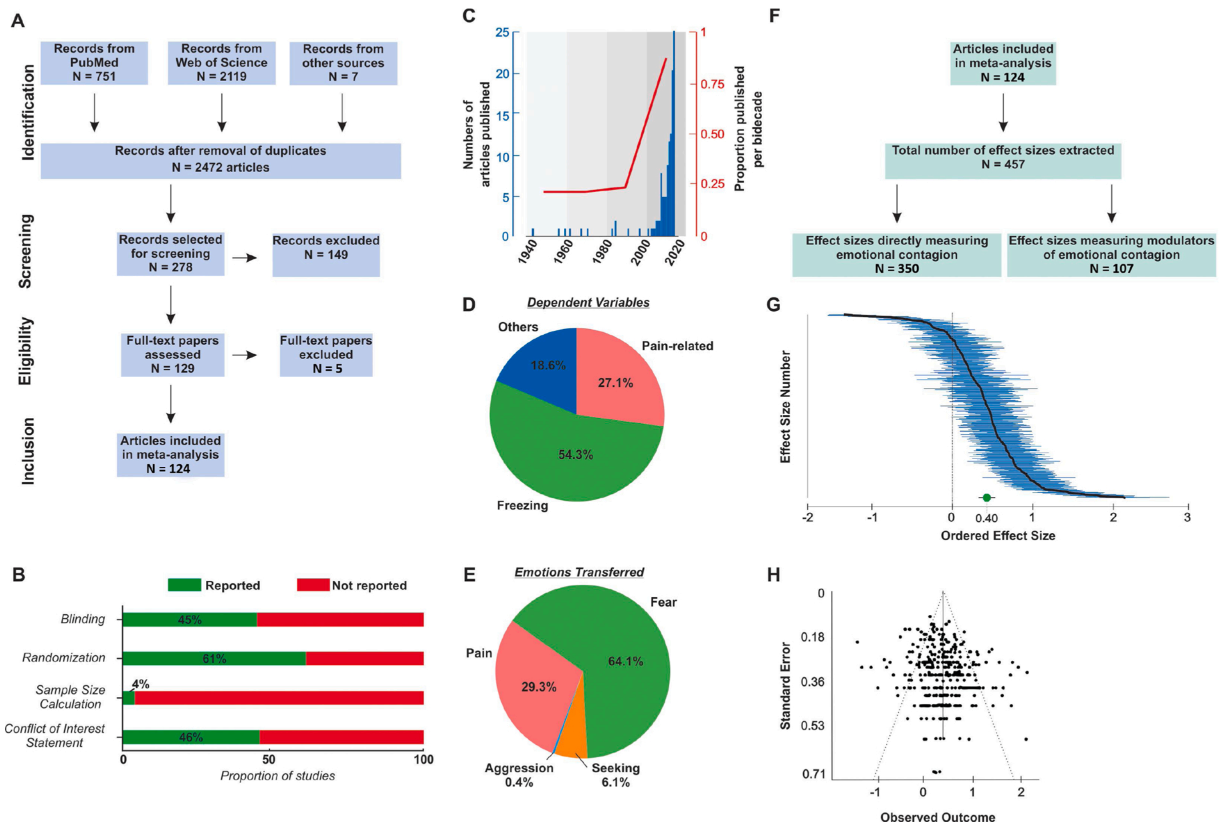


Fig. 2. Descriptive output of the meta-analytic search. (**A**) Flow chart depicting the search strategy together with the number of articles excluded in each step. (**B**) Quality control of the studies scrutinized. Cumulative bar plot shows the proportion of studies that reported blinding, randomization, sample size calculation and statement of conflict of interest in the text. Absence of such details in the article was classified as not reported for that given article. (**C**) Histogram showing the number of studies published between 1940 and 2019. Red trace indicates the proportions of studies published across twenty year time windows. (**D**) Types and proportions of dependent variables collected to quantify emotional contagion. (*E*) Types and proportions of emotions transferred in the selected studies. Categories of emotions use the nomenclature proposed by (Panksepp, 2011). (**F**) Flow chart depicting the number of effect sizes and classification strategy used for analysis. (**G**) Ordered effect sizes (ES, r_z) extracted from all selected studies. Green dot below the sorted scatter plot shows the mean overall effect size together with the standard deviation. (**H**) Funnel plot of the selected studies illustrating potential publication bias, with effect size (r_z) as the observed outcome in the x-axis and standard error in the y-axis.

3.2. *Rats and mice show comparable levels of emotional contagion*

This meta-analysis estimated an overall positive medium effect size for the emotional contagion of rats and mice with a grand mean of r = 0.4 (*z = 15.0 [0.35 to 0.44], p < 0.0001, CI: [0.35 to 0.44]*, Fig. 2G). The robustness of these results was confirmed with a file drawer analysis showing that a large number of studies (*N* = 89,498*)* would be necessary to change the overall effect size to a null effect. Most effect sizes extracted (*N* = *313*) had a positive direction (see methods for criteria), i.e., supporting an increase of emotional contagion. A smaller subset of studies found the opposite effect (*N* = *48*, i.e., reduction in emotional contagion) and few found no effect (*N* = *3*). Moreover, we found no evidence of asymmetry (*kendall's τ* = *0.059, p* = *0.102*) in the funnel plot suggesting that publication bias is highly unlikely (Fig. 2H). Note that the upper part of the funnel plot, representing studies with higher power, is densely populated. It should be noted that all authors witnessed oral communications during conferences and scientific gatherings that pointed out towards an opposite pattern, that is, a strong publication bias in the field of rodent emotional contagion. Caution should be exerted when interpreting this analysis, which has already been suggested as unreliable in certain cases (Lau et al., 2006).

We then compared effect size distributions for each emotion type between rats and mice (Fig. 3A). Despite differences in social structures and general sociability (Archer, 1973), rats and mice showed a similarly high and positive effect size for emotional contagion of fear (rat: $\bar{r}$ = *0.5, CI: [0.4 to 0.59],* mice: $\bar{r}$ =*0.48, CI: [0.4 to 0.54]*) and a lower magnitude (compared to fear) but still positive emotional contagion for pain (rat: $\bar{r}$ =*0.39, CI: [0.17 to 0.62]*, mice: $\bar{r}$ =*0.33, CI: [0.22 to 0.44]).* However, mice were the preferred species to investigate emotional contagion of both fear (mice: *N* = *111*, rat: *N* = *74*) and pain (mice: *N* = *82*, rat: *N* = *22*).

For the other emotional dimensions ("other" sublevel in Fig. 3A), while rats show a similar effect of this category to that measured in fear and pain ($\bar{r}$ =*0.35, CI: [0.19 to 0.51]*), the average effect was close to 0 and non-significant in mice ($\bar{r}$ =*0.08, CI: [-0.17 to 0.32]*). This difference could be driven by the fact that a larger number of studies in mice (71 % in mice vs 15 % in rats) in the "other" category measured emotional contagion by quantifying approach to a negative stimulus. This suggests that: 1) either this measure is a poor indicator of the level of emotional contagion or 2) the paradigms used to extract these measures do not reflect emotional contagion.

3.3. *Strain modulates emotional contagion in mice but not in rats*

Mice: We explored whether certain strains show stronger emotional contagion than others, by clustering effect sizes according to strain (Fig. 3B, C). In mice, we identified four major strains, which accounted for 90 % of the studies: C57BL/6 (*N* = *120*), CD1 (*N* = *49*), 129S1/S4 (*N* = *12*) and CF1 (*N* = *16*). We found a large unbalance of the emotion scrutinized in each mice strain. Only one strain was used in the literature for both pain and fear emotional contagion research (C57BL/6), while all others were used in majority for fear (129S1/S4) or pain research

Table 3
List of included studies (reference), together with publication year, number of effect sizes extracted and that were used for behavioral analysis (ES-Behavior) and number of effect sizes extracted and that were used for physiology analysis (ES-physiology: c-fos and corticosterone).

	Study	Year	ES Behavior	ES -Physiology
1	(Anderson, 1939)	1939	1	0
2	(Davitz and Mason, 1955)	1955	2	0
3	(Church, 1959)	1959	1	0
4	(Korman and Loeb, 1961)	1961	1	0
5	(Baum, 1969b)	1969	2	0
6	(Uno et al., 1973)	1973	2	0
7	(Armario et al., 1982)	1982	1	1
8	(Armario et al., 1983)	1983	0	3
9	(Sales, 1991)	1991	1	0
10	(White and Galef, 1998)	1998	1	0
11	(Livia Terranova et al., 1999)	1999	0	2
12	(Kavaliers et al., 2001a)	2001	2	0
13	(Kavaliers et al., 2001b)	2001	9	0
14	(Kiyokawa et al., 2004a)	2004	1	1
15	(Kavaliers et al., 2005)	2005	6	0
16	(Langford, 2006)	2006	17	0
17	(Knapska et al., 2006a)	2006	1	6
18	(Kiyokawa et al., 2007)	2007	6	15
19	(Wohr and Schwarting, 2007)	2007	6	0
20	(Wöhr and Schwarting, 2008)	2008	1	0
21	(Sadananda et al., 2008)	2008	0	22
22	(Bredy and Barad, 2009)	2009	5	0
23	(Chen et al., 2009)	2009	6	0
24	(Kiyokawa et al., 2009)	2009	3	2
25	(Guzmán et al., 2009)	2009	7	0
26	(Masuda and Aou, 2009)	2009	2	0
27	(Hammerschmidt et al., 2009)	2009	1	0
28	(Wöhr and Schwarting, 2009)	2009	2	0
29	(Gioiosa et al., 2009)	2009	3	0
30	(Kim et al., 2010)	2010	2	0
31	(Jeon et al., 2010)	2010	28	0
32	(Knapska et al., 2010)	2010	7	0
33	(Langford et al., 2010a)	2010	3	0
34	(Bruchey et al., 2010)	2010	1	0
35	(Nakayasu and Kato, 2011)	2011	1	0
36	(Kodama et al., 2011)	2011	1	0
37	(Atsak et al., 2011a)	2011	2	0
38	(Langford et al., 2011)	2011	9	1
39	(Watanabe, 2012)	2012	4	0
40	(Kiyokawa et al., 2012)	2012	1	0
41	(Parsana et al., 2012a)	2012	1	0
42	(Parsana et al., 2012b)	2012	2	0
43	(Kim et al., 2012)	2012	9	0
44	(Sanders et al., 2013)	2013	4	0
45	(Takahashi et al., 2013)	2013	1	5
46	(Kiyokawa et al., 2013)	2013	1	11
47	(Yusufishaq and Rosenkranz, 2013)	2013	2	0
48	(Nowak et al., 2013)	2013	3	0
49	(Masuda et al., 2013)	2013	3	0
50	(Bowen et al., 2013)	2013	1	12
51	(Jung et al., 2013)	2013	1	0
52	(Kashtelyan et al., 2014a)	2014	0	1
53	(Kim et al., 2014)	2014	2	0
54	(Gonzalez-Liencres et al., 2014a)	2014	3	0
55	(Kiyokawa et al., 2014a)	2014	1	4
56	(Jones et al., 2014)	2014	1	0
57	(Li et al., 2014a)	2014	6	1
58	(Hunter, 2014)	2014	1	0
59	(Debiec and Sullivan, 2014)	2014	4	6
60	(Kiyokawa et al., 2014b)	2014	2	2
61	(Willadsen et al., 2014)	2014	1	0
62	(Hodges et al., 2014)	2014	0	2
63	(Nakashima et al., 2015)	2015	2	0
64	(Meyza et al., 2015)	2015	2	18
65	(Fuzzo et al., 2015)	2015	1	0
66	(Harb and Taylor, 2015)	2015	5	0
67	(Hishimura, 2015)	2015	1	0
68	(Suzuki and Lucas, 2015)	2015	2	0
69	(Lee and Noh, 2015)	2015	2	0
70	(Seffer et al., 2014)	2015	9	0
71	(Baptista-de-Souza et al., 2015)	2015	1	1
72	(Martin et al., 2015)	2015	5	0
73	(Carrillo et al., 2015)	2015	2	0
74	(Ito et al., 2015a)	2015	6	2
75	(Watanabe, 2015)	2015	0	2
76	(Watanabe, 2011)	2015	1	1
77	(Smith et al., 2016)	2016	16	4
78	(Nakamura et al., 2016)	2016	4	0
79	(Keum et al., 2016)	2016	23	0
80	(Kiyokawa et al., 2016)	2016	1	0
81	(Mikami et al., 2016)	2016	3	0
82	(Lee and Noh, 2016)	2016	1	0
83	(Ishii et al., 2016)	2016	6	4
84	(Ouda et al., 2016)	2016	0	6
85	(Brill-Maoz and Maroun, 2016)	2016	1	0
86	(Kikusui et al., 2016)	2016	0	2
87	(Jones and Monfils, 2016a)	2016	0	5
88	(Panksepp and Lahvis, 2016)	2016	1	0
89	(Saito et al., 2016)	2016	2	0
90	(Gonzalez-Liencres et al., 2016)	2016	1	0
91	(Chang and Debiec, 2016)	2016	2	0
92	(Liu and Yuan, 2016)	2016	1	0
93	(Jones and Monfils, 2016b)	2016	2	0
94	(Muyama et al., 2016)	2016	6	0
95	(Boivin et al., 2016)	2016	1	0
96	(Colnaghi et al., 2016)	2016	3	0
97	(Janezic et al., 2016)	2016	1	0
98	(Smith et al., 2017)	2017	2	12
99	(Inagaki and Ushida, 2017)	2017	2	0
100	(Twining et al., 2017)	2017	5	0
101	(Choi and Jeong, 2017)	2017	3	0
102	(Kiyokawa and Takeuchi, 2017)	2017	2	0
103	(Chen et al., 2017)	2017	8	1
104	(Fiore et al., 2017)	2017	1	0
105	(Carneiro de Oliveira et al., 2017)	2017	1	0
106	(Pisansky et al., 2017)	2017	9	0
107	(Rivara et al., 2017)	2017	1	0
108	(Pitcher et al., 2017)	2017	28	0
109	(Zhou et al., 2018)	2018	6	0
110	(Hong and Choi, 2018)	2018	4	0
111	(Mulvihill and Brudzynski, 2018)	2018	1	0
112	(Li et al., 2018)	2018	7	0
113	(Kiyokawa et al., 2018)	2018	4	0
114	(Allsop et al., 2018)	2018	5	0
115	(Macrì et al., 2018)	2018	1	0
116	(Sterley et al., 2018)	2018	0	1
117	(Rogers-Carter et al., 2018)	2018	8	0
118	(Sakaguchi et al., 2018)	2018	3	0
119	(Ueno et al., 2018)	2018	6	0
120	(Zaniboni et al., 2018)	2018	3	0
121	(Keum et al., 2018)	2018	10	0
122	(Lu et al., 2018)	2018	3	0
123	Hachiga et al., 2018	2018	1	0
124	(Lichtenberg et al., 2018)	2018	1	0

(CD1, CF1). This unbalanced dataset complicates the interpretation of effect size differences across strains and should therefore be taken with caution. Within these conditions, we found consistent between-strain emotional contagion for fear (Fig. 3B; 129S1/S4: $\bar{r} = 0.48$, *CI: [0.32 to 0.61]*; C57BL/6: $\bar{r} = 0.51$, *CI: [0.43 to 0.51]*), while differences were found for emotional contagion of pain for different strains (CF1: $\bar{r} = 0.76$, *CI: [0.61 to 0.86]*; CD1: $\bar{r} = 0.15$, *CI: [0.02 to 0.27]*; C57BL/6: $\bar{r} = 0.28$, *CI: [0.13 to 0.44]*). We found significant differences in the emotional contagion of pain (Fig. 3C) between C57BL6, CD1 and CF1 ($Q = 57.7$, $p < 0.001$), with CF1 strain showing higher emotional contagion for pain compared to C57BL/6 ($Q = 15.033$, $p < 0.001$) and CD1 ($Q = 23.59$, $p < 0.001$),

In addition to being used for researching a specific emotion, same strains were also exposed to comparable experimental designs (Fig. 3D). For instance, most studies that used C57BL/6 as experimental model

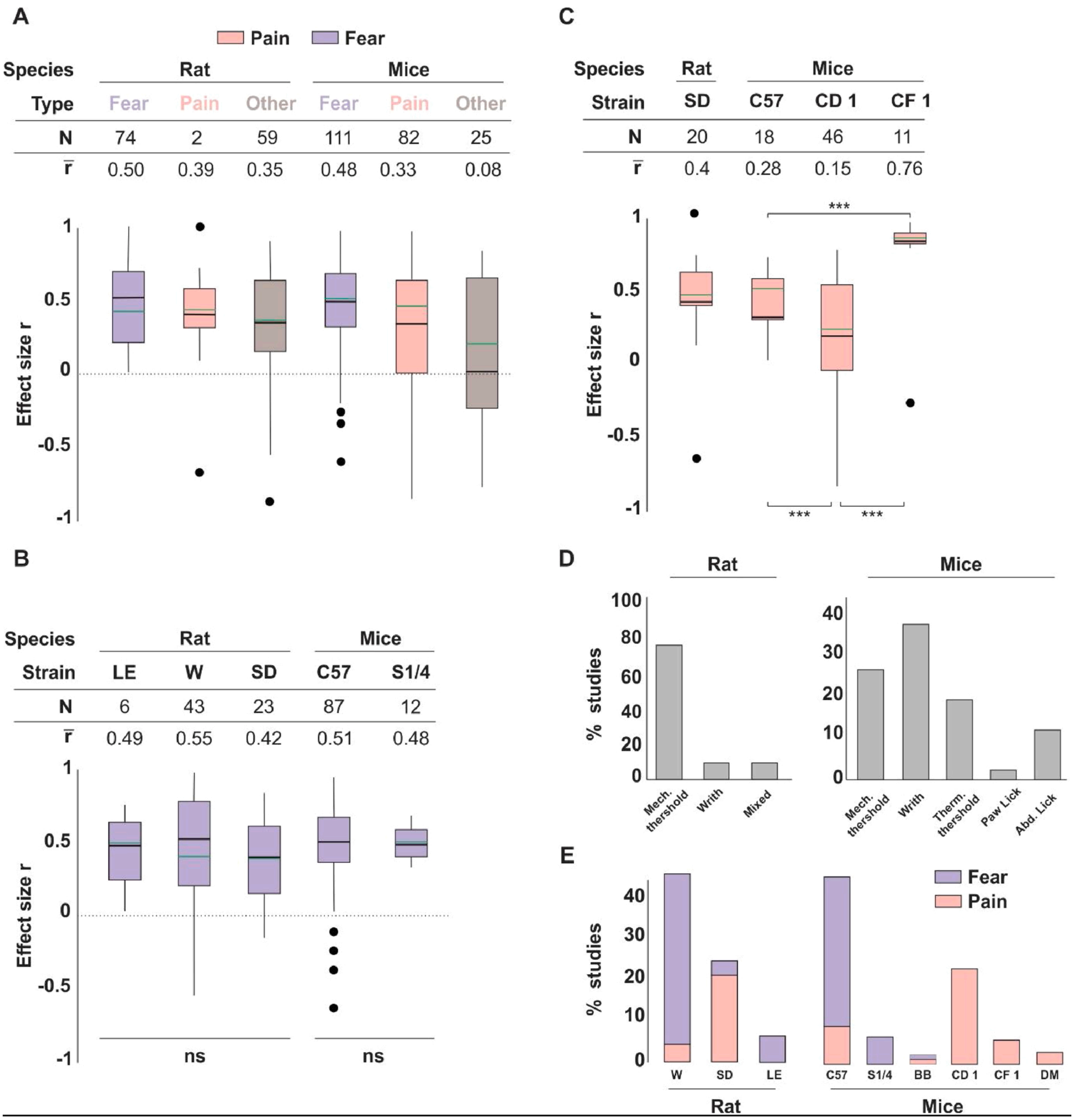


Fig. 3. Rats and mice show comparable levels of emotional contagion. (**A**). Boxplots showing the distributions of effect sizes (r) for rats and mice, separately for fear (blue), pain (red) and other dependent variables (grey). (**B**) Boxplots showing the distributions of effect sizes (r) for different strains of rats and mice in the fear category. **(C)** Boxplots showing the distributions of effect sizes (r) for different strains of rats and mice in the pain category. (**D**) Proportion of studies that used dependent measurements used in the pain category for rats and mice. (*E*) Proportions of studies using fear- and pain-based emotional contagion per strain of mice and rats. For the box plots: 1) The table on top shows the species, strain, number of effect sizes (N) and mean effect size ($\bar{r}$), 2) outliers are indicated by black circles, 3) the black line indicates the mean effect size value ($\bar{r}$), 4) the green line indicates the median effect size (r_m) and in cases where a statistical test was conducted: ***$p<0.001$ and ns=not significant. Abbreviations used: Long Evans [L], Wistar [W], Sprague Dawley [SD], C57BL/6 [c57], 129S1/S4 [S1/S4], Balb/c [BB], Dear mice [DM], Mech Thres = Mechanical Threshold; Writh = Writhing; Mixed = combination of measurements used; Paw Lick = Paw Licking; Abd Lick = Abdominal Licking.

investigated fear processes, while CD1 and CF1 strains were used exclusively for pain research. Moreover, we also observed a misbalance in the dependent variables used to quantify emotional contagion for pain. While fear and anxiety were in great majority measured using freezing, pain was quantified using variables such as mechanical pain or thermal threshold, writhing or licking. It is worthwhile noting that all studies of emotional contagion of pain that used CF1 animals measured thermal sensitivity (e.g., latency to react to hot plate), while studies that used C57BL/6 used paw withdrawal or writhing as an experimental measurement. Thus, the observed strain differences could be due to the type of measurement used, rather than differences in intrinsic characteristics of a given strain. Altogether, these results highlight potential between-strain differences, but also emphasize the need to populate each strain's published data with additional, so far absent experimental variables. More research directly comparing different species and/or strains is needed, although such findings are starting to gather attention in the recent literature (Chen et al., 2009; Keum et al., 2016; Han et al., 2019).

Rats: In rats, we identified three major strains used in the literature: Wistar (N = 68), Sprague Dawley (N = 54) and Long Evans (N = 12). The remaining 12 studies used a range of unconventional strains (Fig. 3A). As observed in mice, there was a strong association between emotion tested and strain used in rats (Fig. 3D). The majority of studies investigating fear processes used Wistar (fear: N = 43; pain: N = 4), while most studies addressing pain processes used Sprague Dawley (fear: N = 23; pain: N = 20). Using the same caution as for the results obtained in mice, our data suggest that all three main strains (SD: $\bar{r}$ =*0.42, CI: [0.28−0.54]*, Wistar: $\bar{r}$ = *0.55, CI: [0.38−0.67]*, LE: $\bar{r}$ =*0.49, CI: [0.25−0.68]*) showed a positive comparable effect size for emotional contagion of fear (Fig. 3B), with no observable strain differences ($Q = 0.017$, $p = 0.895$). This finding matches the results of recent studies (not included in this meta-analysis) that have directly compared multiple strains (Han et al., 2019), and found no significant difference.

Between strains comparison for emotional contagion of pain was not possible (Fig. 3C), because all pain studies were conducted in SD. Within SDs, emotional contagion of pain showed a medium effect size ($\bar{r}$ =*0.4, CI: [0.17−0.65]*). The majority of these studies used mechanical threshold as a measure of pain contagion (Fig. 3D). Another interesting observation was that, overall, there was a clear preference for albino rat strains such as Wistar and Sprague Dawley, over Long Evan rats. This might be due to the general belief that albino rats are calmer and easier to handle than Long Evan rats, or historical preferences for albino strains in the literature. In fact, the first study in our meta-analysis that uses Long Evans to quantify emotional contagion was published in 1998, that is 59 years after the first study using an albino rat (Anderson, 1939). While the number of effect sizes collected in Long Evans is low for emotional contagion of fear and anxiety ($N = 6$) and no effect sizes could be computed for pain studies, the average effect size of studies performed in Long Evans is high and comparable to the ones observed in the two albino strains (Table 4).

Table 4

Summary of results for species and strains. Table shows the name of the modulator (Species and Strain), levels examined for each modulator (Levels), the sublevels investigated (fear, pain and others), the mean effect size value $\bar{r}$ and the confidence interval (CI), the z score value, heterogeneity value as measured by I^2 and sample size (n). Red values indicate non-significant z scores.

Modulator	Levels	Sublevels	$\bar{r}$ mean-CI (low-high)	*z*	I^2 %	n
Species	Rat	Fear	0.5 (0.4−0.59)	8.755	71	74
		Pain	0.39 (0.17−0.62)	3.4	51.2	22
		Other	0.35 (0.19−0.51)	4.3	73.3	50
	Mice	Fear	0.48 (0.4−0.54)	12.9	32.4	111
		Pain	0.33 (0.22−0.44)	5.83	76.5	82
		Other	0.08 (-0.17−0.32)	0.61	59.1	25
Strain	Wistar	Fear	0.55 (0.38−0.67)	6.1	80.4	43
	Sprague Dawley	Fear	0.42 (0.28−0.54)	5.6	52.9	23
		Pain	0.4 (0.17−0.65)	3.23	55	20
	Long Evans	Fear	0.49 (0.25−0.68)	3.85	30.8	6
	C57BL/6	Fear	0.51 (0.43−0.51)	12.33	33	87
		Pain	0.28 (0.13−0.44)	3.6	0	18
	CD1	Pain	0.15 (0.02−0.27)	2.34	78.8	46
	CF1	Pain	0.76 (0.61−0.86)	6.6	44.9	11
	129S1/S4	Fear	0.48 (0.32−0.61)	5.8	0	12

3.4. *Familiarity effect is dependent on the type of emotional stimulus*

How familiarity between two animals influences the contagion of an emotion has been one of the most investigated variables in this type of paradigms (Kavaliers et al., 2005; Knapska et al., 2010; Jones et al., 2014; Chen et al., 2017; Pisansky et al., 2017; Pitcher et al., 2017; Zhou et al., 2018; Gonzalez-Liencres et al., 2014b; Langford et al., 2006, 2010b; Li et al., 2014b). The accepted hypothesis in the field is that animals that are familiar with each other will have a stronger emotional contagion response (here coded as a positive effect size). Interestingly, when grouping all studies, we found no consistent differences in transfer of emotions of familiar and unfamiliar cage mates for mice or rats (familiar vs unfamiliar; mice fear: $Q = 0.794$, $p = 0.373$; mice pain: $Q = 0.19$, $p = 0.663$; rat fear: $Q = 0.642$, $p = 0.423$; rat pain: $Q = 0.029$, $p = 0.865$, Table 5, Fig. 4A). One possibility for this negative finding is the large between-study differences in familiarity length (number of days animals were together prior to test, total range: *[1 to 196] days*, $\bar{x}$ = *17.9*). We thus ran an additional analysis where we only included studies where dyads were familiar for at least 6 days (median familiarity value of the total range). This analysis yielded similar non-significant results (rat fear: $Q = 1.778$, $p = 0.182$; rat pain: $Q = 0.029$, $p = 0.865$; mice fear: $Q = 0.257$, $p = 0.612$; mice pain: $Q = 2.014$; $p = 0.156$). To further examine the role of familiarity in emotional contagion, we looked at how the relationship length (cutoff at 100 days to exclude extreme values) correlated with the contagion response for fear (Fig. 4B). No enough data was available to run the equivalent analysis for pain contagion. While mice showed a trend in a positive relationship between time spent together and fear contagion levels ($\bar{r}$ =*0.29, p* = *0.07*), rats showed a strong negative correlation between familiarity length and emotional contagion response ($\bar{r}$ =*-0.49, p* = *0.02*). However, it should be noted, that there was a difference in the range of relationship days used for studies done in rats vs mice (Fig. 4C), with studies in mice using a much more extensive range of relationship days. That familiarity might modulate emotional contagion differently in mice and rats requires additional scrutiny, with experiments specifically designed to test this parameter.

In line with this idea, we conducted a separate analysis using studies which specifically tested the role of familiarity in rats (Armario et al., 1982; Knapska et al., 2010; Jones et al., 2014; Rogers-Carter et al., 2018; Li et al., 2014b) and mice (Kavaliers et al., 2005; Langford, 2006; Martin et al., 2015; Gonzalez-Liencres et al., 2016; Pisansky et al., 2017; Pitcher et al., 2017; Zhou et al., 2018; Ueno et al., 2018; Langford et al., 2010b). These studies showed that while mice have a stronger pain contagion response to a familiar animal compared to an unfamiliar one ($Q = 20.425$, $p < 0.001$), this familiarity effect was extinguished for fear contagion ($Q = 16.7$, $p = 0.164$). Interestingly, except for one, studies that found increased pain contagion used abdominal pain as the dependent variable, indicating that perhaps increased response to a familiar in distress depends on the type of pain stimulus. To test this idea, we repeated the familiarity analysis with studies that investigated pain contagion in mice (not enough studies in rats), dividing the response based on the type of pain. Confirming our hypothesis, we found that only in studies using contagion to abdominal pain (i.e., writhing) mice showed an increased response to familiar compared to unfamiliar conspecific ($Q = 13.557$, $p < 0.001$), while there was no difference in the response to familiar vs unfamiliar conspecifics in other types of pain. This differential effect based on the type of emotional stimulus could be driven by differences in the ecological validity of the stimulus (i.e., mice are more likely to witness another with abdominal pain than being fearful due to footshocks).

3.5. *Age modulates differentially fear contagion in rats and mice*

The age of animals used in the emotional contagion literature had a large range for both rats (total range *[9–275] days*, $\bar{x} = 66.13$) and mice (total range *[21–330] days*, $\bar{x}$ = *77.7*) (Fig. S1). A linear regression

Table 5

Summary of results for familiarity, sex and housing. Table shows the name of the modulator (e.g., Familiarity), Species (Rat and mice), levels examined for each modulator (Levels), the sublevels investigated (e.g. fear), the mean effect size value $\bar{r}$ with the confidence interval (CI), the z score value, heterogeneity value as measured by I^2 and sample size (n). Red values indicate non-significant z scores, or modulators with a sample size (n) lower than 5.

Modulator	Species	Levels	Sublevels	$\bar{r}$ mean-CI (low-high)	z	I^2 %	n
Familiarity	Rat	Unfamiliar	Fear	0.58 (0.41–0.71)	5.75	81.2	35
		Cagemates	Fear	0.42 (0.27–0.55)	5.18	51.7	19
		Unfamiliar	Pain	0.41 (0.001-0.71)	1.97	14.1	3
		Cagemates	Pain	0.39 (0.16–0.57)	3.29	54.4	19
	Mice	Unfamiliar	Pain	0.41 (0.3–0.49)	3.1	81	44
		Cagemates	Pain	0.42 (0.33–0.51)	5.66	62.1	36
		Unfamiliar	Fear	0.29 (0.11–0.45)	7.48	27.3	39
		Cagemates	Fear	0.32 (0.22–0.42)	8.3	32.7	57
		Couples	Fear	0.52 (0.26–0.64)	3.5	45.9	6
Sex	Rat	Female	Fear & Pain	0.43 (0.25–0.59)	4.2	17.4	6
		Male	Fear & Pain	0.48 (0.37–0.57)	8.3	72.2	88
	Mice	Female	Fear & Pain	0.57 (0.39–0.7)	5.52	0	4
		Male	Fear & Pain	0.42 (0.35–0.49)	10.6	65.3	160
Housing	Rat	Alone	Fear	0.65 (0.47–0.77)	5.7	80	25
		Group	Fear	0.41 (0.29–0.52)	6.2	66.2	47
		Alone	Pain	–	–	–	0
		Group	Pain	0.38 (0.17–0.55)	3.4	51.2	22
	Mice	Alone	Fear	0.57 (0.35–0.79)	5.1	27.9	7
		Group	Fear	0.43 (0.36–0.49)	11	34.7	96
		Alone	Pain	0.62 (0.5–0.73)	7.7	43.3	31
		Group	Pain	0.17 (0.05–0.27)	2.7	77.9	51

analysis (Fig. 4D) showed that while in rats age is negatively correlated with the amount of fear contagion (*$\bar{r}$ = -0.32, p = 0.02*), the opposite is true in mice (*r = 0.37, p = 0.0001*). This effect could reflect species specific age-related changes in additional factors such as animal size and weight (as animals get older, they gain more weight), animal cognition and behavior.

3.6. Sex does not modulate emotional contagion in rats and mice

Given the low number of effect sizes for females, we kept the analysis investigating an effect of sex on emotional contagion at the species level. We find no evidence for an effect of sex on emotional contagion of pain or fear in rats or mice (Fig. 4E, Table 5; *all $p > 0.05$)*. In addition, qualitative examination (not enough effect sizes for a quantitative analysis) of studies that specifically looked at sex effects on contagion, revealed no clear effect of sex on contagion of fear nor pain. This is in agreement with findings from a recent study showing that although female rats freeze less compared to males when experiencing shock, the fear contagion response is comparable between males and females (Han et al., 2019b). It is important to note that overall, only 3.5 % of all the studies used females, 10.1 % used both females and males and 86.4 % used males, which highlights how underrepresented is the use of females in studies investigating emotional contagion in rodents. Although, this bias is not specific to empathy research, it is worth underscoring the severity of the problem and highlighting the importance of using both females and males, which recent studies have highlighted (Pisansky et al., 2017). Hence, our results on sex should be taken with caution, since we could not dwell deeply into the role of this effects due to lack of data points.

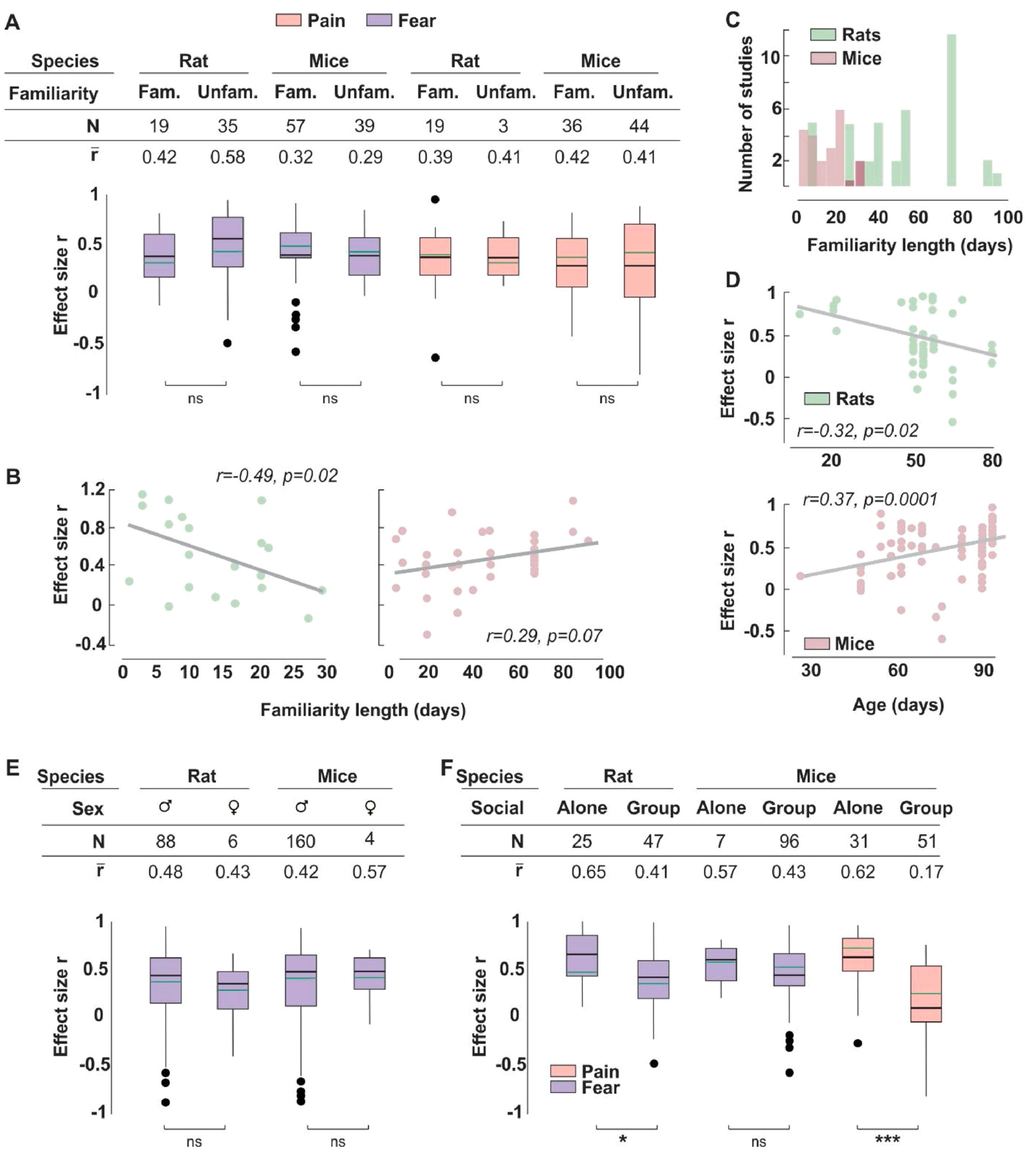
3.7. Single housing potentiates emotional contagion in rats and mice

In behavioral paradigms investigating social phenomena, whether animals are single or group-housed before or during the experimental measures is often seen as a relevant factor and reported in the method section. However, this variable has not received much attention in studies investigating emotional contagion and was included as a potential modulating factor in this meta-analysis (Table 5, Fig. 4F). We found that compared to group-housed rats, single-housed rats displayed higher levels of emotional contagion of fear (rat alone: *$\bar{r}$ = 0.65, CI: [0.47 to 0.77]*; rat group: *$\bar{r}$ =0.41 CI: [0.29 to 0.52]*; rat alone vs group *Q = 5.906, p = 0.015*]. In mice, although grouped-house animals showed higher levels of emotional contagion of fear compared to single-housed mice, this difference did not reach statistical significance (mice alone: *$\bar{r}$ = 0.57 CI: [0.35 to 0.79]*; mice group: *$\bar{r}$ =0.43, CI: [0.36 to 0.49]*; mice alone vs group *Q = 0.724, p = 0.395]*).

In paradigms measuring emotional contagion for pain, we found that effects in single-housed mice more than tripled compared to group-housed mice (mice alone: *$\bar{r}$ =0.62, CI: [0.5–0.73]*; mice group: *$\bar{r}$ =0.17, CI: [0.05–0.27], Q = 24.247, $p < 0.001$*) (Table 5, Fig. 4F). This increased contagion could be due to the fact that social isolation triggers a series of physiological changes that increase sensitivity to anxiety and fear-related behaviors (Lukkes et al., 2009). Also, social isolation might make conspecifics more salient, thereby boosting the reaction to other's emotions.

3.8. Differences in testing related parameters can affect emotional contagion

Pre-exposure: It is a common view that first-hand experience with a distress-causing stimulus, can potentiate the emotional contagion response to that stimulus. To take this aspect into account, the behavioral design of paradigms testing emotional contagion sometimes include a *pre-exposure* session, in which the animal that will witness the emotion of another, experiences itself the stimulus inducing that emotion (Fig. 5A, Table 6). In rats, we found that pre-exposure almost doubles the emotional contagion response to fear ((Fig. 5B; not pre-exposed: *$\bar{r}$ =0.29, CI: [0.12 to 0.45]*; pre-exposed: *$\bar{r}$ = 0.55, CI: [0.43 to 0.64]*; comparison: *Q = 4.058, p = 0.044*). For pain contagion, not pre-exposed animals had a slightly higher emotional contagion response than pre-exposed animals (*$\bar{r}$ =0.32, CI: [-0.8 to 0.94]*; pre-exposed: *$\bar{r}$ =0.42, CI: [0.27 to 0.55]*), but the low number of published studies that used pre-exposure in pain paradigms prevented us from performing statistical comparisons. In contrast, pre-exposure in mice had no effect on contagion to fear (not pre-exposed: *$\bar{r}$ =0.44, CI: [0.37 to 0.5]*; pre-exposed: *$\bar{r}$ =0.48, CI: [0.35 to 0.58]*; comparison: *Q = 0.177, p = 0.674*) or pain (not pre-exposed: *$\bar{r}$ =0.32, CI: [0.2 to 0.43]*; pre-exposed: *$\bar{r}$ =0.23, CI: [0.14 to 0.54]*; comparison: *Q = 0.098, p = 0.754*). This lack of pre-exposure effect in mice might explain why this session is rarely included in mice studies (13 % of studies), in comparison to rat studies (66 % of studies). The effect of pre-exposure in contagion of fear we find in rats, matches the finding of studies that explicitly tested for this effect



A

Species	Rat		Mice		Rat		Mice	
Familiarity	Fam.	Unfam.	Fam.	Unfam.	Fam.	Unfam.	Fam.	Unfam.
N	19	35	57	39	19	3	36	44
r̄	0.42	0.58	0.32	0.29	0.39	0.41	0.42	0.41

E

Species	Rat		Mice	
Sex	♂	♀	♂	♀
N	88	6	160	4
r̄	0.48	0.43	0.42	0.57

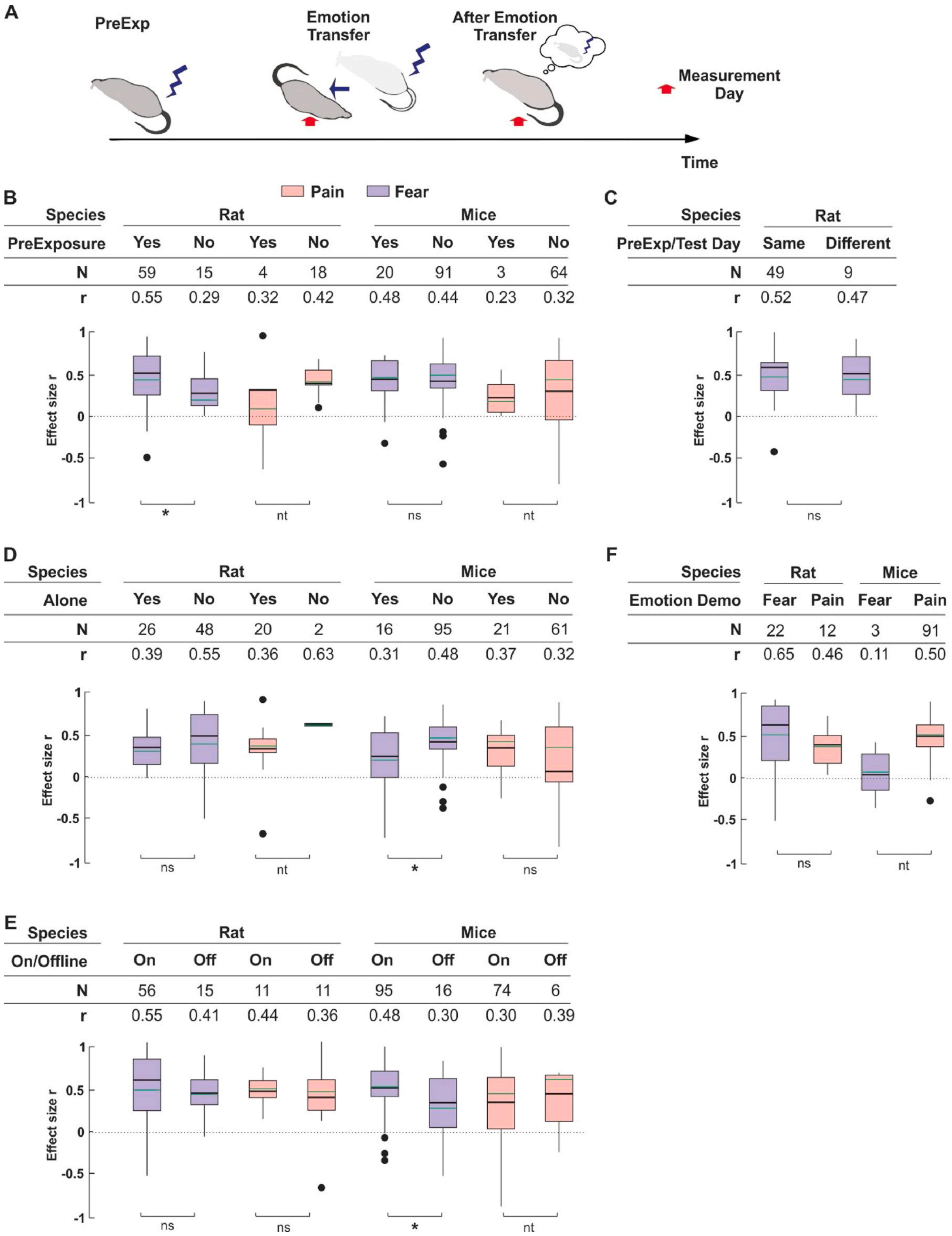
F

Species	Rat		Mice			
Social	Alone	Group	Alone	Group	Alone	Group
N	25	47	7	96	31	51
r̄	0.65	0.41	0.57	0.43	0.62	0.17

Fig. 4. Effect of familiarity, age, sex and housing conditions on emotional contagion. (**A**) Box plot showing the distribution of effect sizes (r) for familiar (fam) and unfamiliar (unfam) rats and mice. (**B**) Linear regression showing relationship between familiarity length (number of days test animals were in contact with each other) and the standardized effect size for rats (green) and mice (red). (**C**) Histogram showing the distribution of relationship days used for rat (green) and mice (red) studies. (**D**) Linear regression showing the relationship between animal age in days and effect size (r) for rats (green) and mice (red) for fear contagion. (*E*) Box plot showing the distribution of effect sizes (r) for male (♂) and female (♀) rats and mice for emotional contagion of fear. (**F**) Box plots showing the distribution of effect sizes (r) for rats and mice when animals were housed alone vs in groups. Graphs show the effect sizes separated for contagion of fear (blue) and pain (red). For the box plots1) outliers are indicated by black circles, 2) the black line indicates the mean effect size value ($\bar{r}$), the green line indicates the median effect size value (r_m) and in cases where a statistical test was conducted, *$p<0.05$, ***$p<0.001$ ns=not significant.

(Atsak et al., 2011b; Han et al., 2019). In contrast, in mice the effect of pre-exposure is not clear, as some studies that explicitly examined the role of pre-exposure find that it is necessary to pre-expose animals (Sanders et al., 2013), while other studies, in agreement with our results, find that it is not required in mice (Kavaliers et al., 2001b, 2005).

One possibility that might account for the between-species difference in pre-exposure effect is a systematic difference in experimental procedures. For instance, if the paradigms used to test emotional contagion had differences in the timing of pre-exposure (exposure to stimuli alone) relative to interaction (transfer of emotion) and test (measure of dependent variable). Although, there were a few studies with a substantial delay between pre-exposure and test, the majority of studies in both rats and mice conducted pre-exposure and test on the same day (Table 6, “PreExp Day”). Moreover, there was no effect of delay between pre-exposure and test in mice or rat (Fig. 5C), suggesting that additional underlying variables might drive the between species difference



B

Species	Rat				Mice			
PreExposure	Yes	No	Yes	No	Yes	No	Yes	No
N	59	15	4	18	20	91	3	64
r	0.55	0.29	0.32	0.42	0.48	0.44	0.23	0.32

C

Species	Rat	
PreExp/Test Day	Same	Different
N	49	9
r	0.52	0.47

D

Species	Rat				Mice			
Alone	Yes	No	Yes	No	Yes	No	Yes	No
N	26	48	20	2	16	95	21	61
r	0.39	0.55	0.36	0.63	0.31	0.48	0.37	0.32

F

Species	Rat		Mice	
Emotion Demo	Fear	Pain	Fear	Pain
N	22	12	3	91
r	0.65	0.46	0.11	0.50

E

Species	Rat				Mice			
On/Offline	On	Off	On	Off	On	Off	On	Off
N	56	15	11	11	95	16	74	6
r	0.55	0.41	0.44	0.36	0.48	0.30	0.30	0.39

Fig. 5. Pre-exposure and testing conditions influence emotional contagion in rats and mice. (**A**) Diagram summarizing the timing of different experimental events. In some studies test animals were pre-exposed (PreExp) to the emotion eliciting stimuli prior to emotion transfer (ET). During the ET, the target animal witnessed the response of another animal to an emotional eliciting stimulus. The measurement of emotional contagion was done online during ET or offline after ET. (**B**) Box plot showing the distribution of effect sizes (r) for pre-exposed and not pre-exposed rats and during contagion of fear (blue) and pain (red). (**C**) Box plot showing the distribution of effect sizes (r) for rats that had the pre-exposure procedure on the same day (Same) and different day (Different) as the emotion (fear) transfer session. (**D**) Box plot showing the distribution of effect sizes (r) for rats and mice that were tested alone and not alone during contagion of fear (blue) and pain (red). (**E**) Box plots showing the distribution of effect sizes (r) for rats and mice that were measured during (online) or after the emotion transfer (offline). (**F**) Box plot showing the distribution of effect sizes (r) for rats and mice that witnessed demonstrators experience fear or pain emotions when the dependent variable measured was fear (blue colouring). For the box plots: 1) outliers are indicated by black circles, 2) black line indicates the mean effect size value ($\bar{r}$) and 4) green line indicates median effect size value (r_m). For comparisons: $^*p<0.05$, NS=not significant and nt=not tested (for comparisons in which one of the groups had less than 5 studies).

Table 6

Summary of results for test related factors. Table contains the name of the modulator: 1) whether an animal experienced pre exposure or not (PreExp), 2) whether an animal was tested alone or not (Testing condition), 3) emotion transferred during interaction (emotion transferred), 4) time of the pre-exposure relative to emotional transfer (PreExp time), and 5) time of measurement relative to emotional transfer (measure time). In addition, the table contains information about the Species (Rat and mice), levels examined for each modulator (Levels), the sublevels investigated (e.g. fear), the mean effect size value r̄ with the confidence interval (CI), the z score value, heterogeneity value as measured by I^2 and sample size (n). Red values indicate non-significant z scores, or modulators with a sample size (n) lower than 5.

Modulator	Species	Levels	Sublevels	r̄ mean-CI (low-high)	z	I^2 %	n
PreExp	Rat	Pre-exp	Fear	0.55 (0.43–0.64)	8.1	75	59
		No pre-exp	Fear	0.29 (0.12–0.45)	3.2	43	15
		Pre-exp	Pain	0.32 (-0.8–0.94)	0.45	90	4
		No pre exp	Pain	0.42 (0.27–0.55)	5.22	0	18
	Mice	Pre-exp	Fear	0.48 (0.35–0.58)	6.9	19	20
		No pre-exp	Fear	0.44 (0.37–0.5)	11.2	34.7	91
		Pre-exp	Pain	0.23 (0.14–0.54)	1.21	67	3
		No pre exp	Pain	0.32 (0.2–0.43)	4.99	81	64
PreExp Day	Rat	Same day	Fear	0.52 (0.4–0.64)	6.8	75.5	49
	Diff day	Fear	0.47 (0.17–0.69)	2.97	75.6	9	
		Same day	Pain	0.32 (-0.8–0.94)	0.45	90.1	4
		Diff day	Pain	–	–	–	0
	Mice	Same day	Fear	0.46 (0.27–0.6)	4.59	26.2	13
		Diff day	Fear	–	–	–	0
		Same day	Pain	–	–	–	0
		Diff day	Pain	–	–	–	0
Testing condition	Rat	Alone	Fear	0.39 (0.26–0.5)	5.8	46.8	26
		Not alone	Fear	0.55 (0.41–0.67)	6.7	78.3	48
		Alone	Pain	0.36 (0.11–0.6)	2.86	52.8	20
		Not alone	Pain	0.63 (0.24–0.85)	0	2.88	0
	Mice	Alone	Fear	0.31 (0.09–0.53)	2.72	73.5	16
		Not alone	Fear	0.48 (0.43–0.53)	15.3	0	95
		Alone	Pain	0.37 (0.21–0.52)	4.6	14.5	21
		Not alone	Pain	0.32 (0.19–0.45)	4.8	81.2	61
Emotion Transferred	Rat	Dem Fear	Fear	0.65 (0.42–0.8)	4.75	85.8	22
		Dem Pain	Fear	0.46 (0.27–0.55)	4.65	35.5	12
	Mice	Dem Fear	Fear	0.11(0.27–0.46)	2	0.54	25.3
		Dem Pain	Fear	0.5 (0.45–0.55)	16.4	0	91
Measurement Time	Rat	Online	Fear	0.55 (0.41–0.65)	7.34	76.9	56
		Offline	Fear	0.41 (0.26–0.52)	5.5	30.1	15
		Online	Pain	0.44 (0.36–0.51)	10.3	0	11
		Offline	Pain	0.36 (0.09–0.7)	1.59	73.4	11
	Mice	Online	Fear	0.48 (0.43–0.53)	15.3	0	95
		Offline	Fear	0.3 (0.08–0.49)	2.72	73.5	16
		Online	Pain	0.3 (0.19–0.4)	5.19	77.1	74
		Offline	Pain	0.39 (0.06–0.64)	2.31	59.5	6
Sensory Modality	Rat	All	Fear	0.51 (0.4–0.6)	7.76	75.35	62
		Not all	Fear	0.41 (0.22–0.57)	4	18.8	10
		All	Pain	0.39 (0.17–0.57)	3.37	53.15	21
		Not all	Pain	–	–	–	0
	Mice	All	Fear	0.45 (0.39–0.5)	12.8	32.7	109
		Not all	Fear	0.37 (0.32–0.8)	1.06	47.8	2
		All	Pain	0.32 (0.2–0.43)	5.01	81.2	62
		Not all	Pain	0.22 (-0.07–0.48)	3	57	7

reported earlier.

Because the observed difference was in fear contagion paradigms, which commonly use shocks as the stimulus, it is possible that this between-species effect was driven by differences in the shocking protocol. Indeed, we found that during pre-exposure, while there were no differences in the shock intensity, inter-stimulus intervals or the time when the pre-exposure was done relative to test (for all comparisons, two-tailed t-test, $p > 0.05$), rats were exposed to a larger number of shocks compared to mice (mice: $\bar{x} = 1.86$, SEM = 0.59; rat: $\bar{x} = 5.22$, SEM = 3.66, two-tailed t-test, $p = 0.02$). Moreover, we also found species differences in shock parameters during emotion transfer, with mice having a significantly higher number of shocks (mice: $\bar{x} = 12.7$, SEM = 1.75; rat: $\bar{x} = 5.52$, SEM = 3.18, two-tailed t-test, $p = 0.0003$) and shorter inter-stimulus interval (mice: $\bar{x} = 27.3$, SEM = 8.1; rat: $\bar{x} = 170$, SEM = 64.2, two-tailed t-test, $p = 0.047$). Combined, these differences could account for the species difference in pre-exposure effect as well as the lack of consensus in the pre-exposure effect in mice. In other words, if the shocking protocol used during emotion transfer is intense enough, as typically observed in studies using mice, it might be sufficient to elicit a contagion response without the need of a pre-exposure.

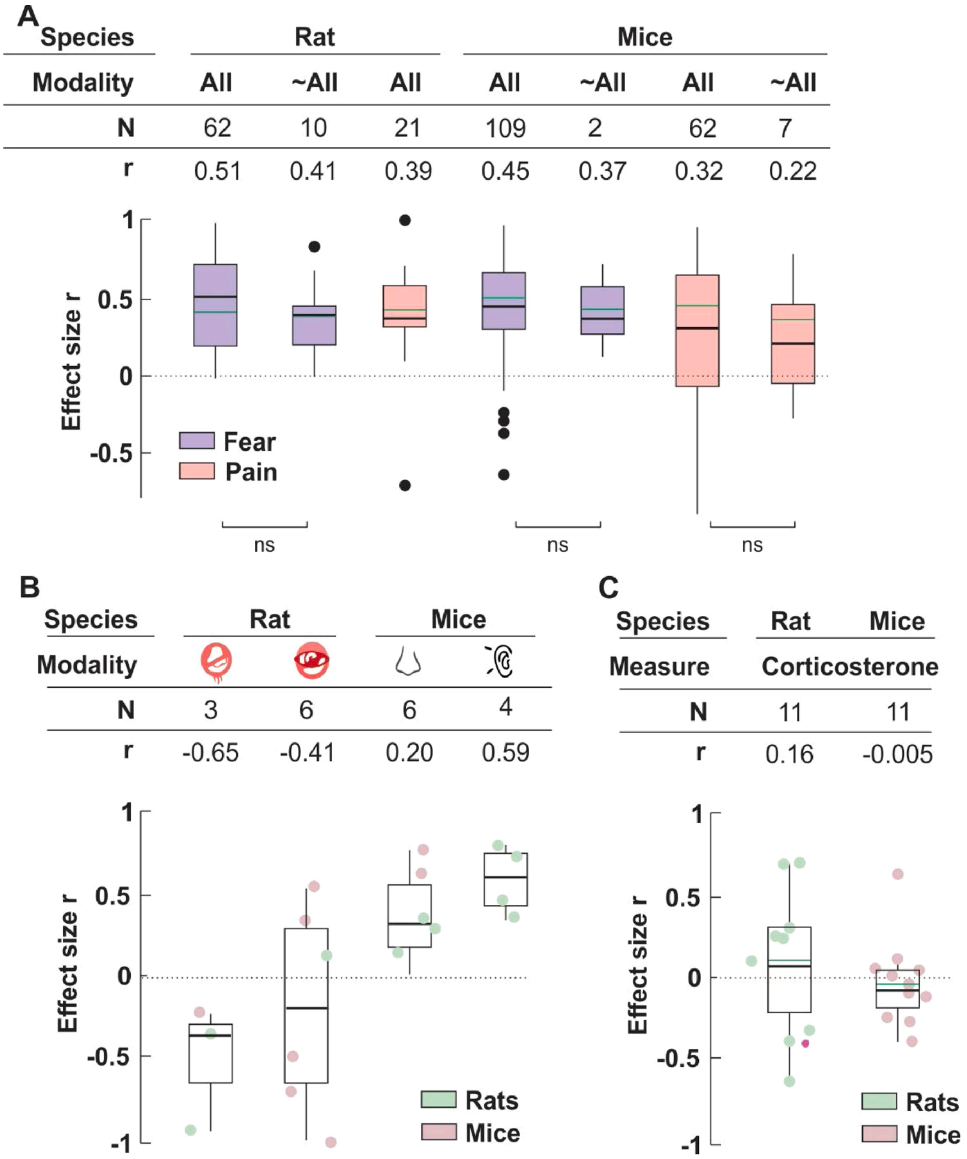
Social testing situation: While in some experiments the measurement of contagion was performed when the animal was alone (rat: $N = 46$; mice: $N = 37$), in the majority of studies the measurement was performed when the animal was in a social context (rat: $N = 50$, mice: $N = 156$; Table 6, 'Testing condition'). One example of such paradigm was exposing a target animal to emotions of a conspecific, and then separating the target animal and testing the emotional contagion response in a socially isolated situation (alone), to extract measures such as pain threshold or anxiety levels (Smith et al., 2016). We found that mice tested alone showed significantly reduced fear contagion compared to animals that were tested in together with a demonstrator animal (Fig. 5D; mice alone: $\bar{r} = 0.31$, *CI: [0.09;0.53]*, mice tested in group: $\bar{r} = 0.48$, *CI: [0.43 to 0.53]*; comparison: $Q = 5.988$, $p = 0.014$). In rats, we also observed increased fear contagion in group vs alone-tested animals, however this difference did not reach statistical significance (rat alone: $\bar{r} = 0.39$, *CI: [0.26 to 0.5]*; rat tested in group, $\bar{r} = 0.55$, *CI: [0.41 to 0.67]*; comparison: $Q = 3.023$, $p = 0.082$). However, being alone or in group during testing procedures seemed to be only important for contagion of fear, since the social testing conditions had no effect in paradigms probing the contagion of pain (mice alone: $\bar{r} = 0.37$, *CI: [0.21 to 0.52]*, mice tested in group: $\bar{r}$ =*0.32, CI: [0.19 to 0.45]*; comparison: $Q = 0.180$, $p = 0.671$; not enough data in rats).

Further, we considered whether the “alone” testing might be homologous to measurements that happened after emotional transfer. It that were true, that mice tested in an isolated situation show a reduced contagion response could be driven not by the social situation, but by the timing of the contagion measure relative to emotion transfer. We categorized this timing as online, when the contagion measure was during the emotional transfer and offline, when the contagion measurement happened after the emotion transfer (Fig. 5E). Overall, in most studies emotional contagion was measured during emotional transfer (i.e., online measure; 70 % of rat studies, and 88 % of mice studies; Table 6). We find that mice show stronger fear contagion when the contagion measure happens during emotional transfer ($Q = 6$, $p = 0.014$). This effect was not dependent on the emotion experienced by the demonstrator (Fig. S2).

Sensory Modalities: Emotional contagion depends on an effective communication of the affective state from the source of the emotion to the receiver. The receiver gathers all information about the source through its sensorial system but are all sensory modalities equally effective is a question that remains unclear.

We found that emotional contagion was higher when all sensory modalities were recruited during emotional transfer, compared to studies in which the measured animal was missing one or more sensory modalities (e.g., anosmic animals), although this difference did not reach statistical significance in rats (fear-all: $\bar{r}$ = *0.51, CI: [0.4 to 0.6]*, fear not all: $\bar{r}$ =*0.41, CI: [0.22 to 0.57]*; not enough data for pain, $p < 0.05$ for all) or in mice (fear-all: $\bar{r}$ =*0.45, CI: [0.39 to 0.5]*; fear not all: $\bar{r}$ =*0.37, CI: [0.32 to 0.8]*; pain-all: $\bar{r}$ =*0.32, CI: [0.2 to 0.43]*; pain not all: $\bar{r}$ =*0.22, CI: [-0.07 to 0.48]*), $p < 0.05$ for all).

Similarly, to other modulators, a significant amount of studies (N = 21) were specifically designed to investigate the effect of certain sensory modalities in the transfer of emotions (Fig. 6B). Among those studies, we found that animals with blocked olfaction (rat: $\bar{r}$ =*-0.65, CI: [-0.94 to 0.21]*; no mice data) or vision (mice: $\bar{r}$ =*-0.41, CI: [-0.92 to 0.6]*, no rat data) had an overall reduction in the contagion of fear and pain. Given these results we would expect that studies in which a single modality was used to convey information about the emotional level of a conspecific, little or no contagion would be observed. In contrast to our expectations, studies in which emotional transfer was done solely through the olfactory (rat: $\bar{r}$ =*0.20, CI: [-0.07 to 0.48]*, mice: $\bar{r}$ =*0.69, CI: [0.44 to 0.85]*) or auditory channel (i.e., USV, mice: $\bar{r}$ = *0.59, CI: [0.35 to 0.77]*, no rat data) showed increased contagion when compared to controls in which a non-emotional stimulus was used as control. However, because



Species	Rat			Mice			
Modality	All	~All	All	All	~All	All	~All
N	62	10	21	109	2	62	7
r	0.51	0.41	0.39	0.45	0.37	0.32	0.22

Species	Rat		Mice	
Modality				
N	3	6	6	4
r	-0.65	-0.41	0.20	0.59

Species	Rat	Mice
Measure	Corticosterone	
N	11	11
r	0.16	-0.005

Fig. 6. Relationship of sensory modality and corticosterone with emotional contagion. (**A**) Box plot showing the distribution of effect sizes (r) for rat (pink background) and mice (green background) and for contagion of fear (blue dots) and of pain (red dots) when all sensory modalities (All) where intact during emotional transfer and when one or more of the sensory modalities was blocked (~All). (**B**) Box plot showing the distribution of effect sizes (r) measuring levels of emotional contagion following sensory modality manipulations for rats (pink dots) and mice (green dots), from left to right: studies that blocked smell, studies that blocked vision, studies that only used smell and studies that only used sound, specifically USV. (**C**) Box plot showing the distribution of effect sizes for rat (left, pink) and mice (right, green) for corticosterone levels in experimental animals compared to controls. For the box plots: 1) The number of effect sizes is depicted below each boxplot distribution, 2) outliers are indicated by black circles, 3) black line in each boxplot indicates the mean effect size value ($\bar{r}$) and 4) green line indicates the median effect size value (r_m). For comparisons: *p<0.05, NS=not significant and nt=not tested (for comparisons in which one of the groups had less than 5 studies).

of the small number of animals and variability in the data, we have to take these results with caution. Together this suggest that emotional contagion is a multi-sensory phenomenon, in which single modalities can suffice in conveying emotional contagion, but where full effect strength is reached by a multi-modality transfer of emotion.

3.9. Physiological measures of emotional contagion

Corticosterone: To examine whether contagion of fear and pain also results in increased levels of stress some studies measured corticosterone levels in the target animals following emotional transfer (Fig. 6C). Together these studies show inconsistent changes in corticosterone levels in mice ($\bar{r}$ =*-0.005, CI: [-0.06 to 0.07]*) and rats ($\bar{r}$ =*0.16, CI:[-0.1 to 0.4]*) following interaction with a distress conspecific. The large variability in the effect sizes suggests that there is no simple relationship in the transfer of emotional distress and fluctuations in corticosterone level.

3.10. C-fos activation patterns reveal a cortico-limbic circuit strongly involved in emotional contagion in the rodent brain

In order to identify which brain structures play a role in emotional contagion, we quantified effect sizes in experiments reporting c-fos in rats and mice collected after emotional transfer (Table 3). The proto-oncogene c-fos is an immediate early gene expressed in neurons in response to various stimuli and is commonly used as a marker of neuronal activation. Given the small amount of c-fos related effect sizes, we limited our analysis to differentiating rats and mice, while not including any other sub-levels (e.g., strain, familiarity). Among the papers selected for this meta-analysis, N = 16 papers reported c-fos data, with a majority of them using rats (rats: N = 13, mice, N = 3). The effect sizes were computed for each brain structure reported in the studies (Fig. 7A). In rats, a large number of effect sizes (N = 112) allowed to perform meta-analytics on 22 brain structures, while one brain area (lateral preoptic area), associated with only 1 effect size, was not included in the analysis (Fig. 7A, red marking). In rats, the results highlight a cluster of activation in medial frontal areas, with strong c-fos activation pattern in the anterior cingulate and prelimbic cortices, and to a lesser extend infralimbic cortices (Table 7). A second cluster of activation grouped subcortical areas containing mainly the striatum (nucleus accumbens, NAcc) and specific amygdala nuclei, in particular the basolateral and lateral nuclei (Fig. 7B).

In mice, the limited number of effect sizes (N = 32) associated with brain areas precluded us from computing meta-analytics in 10 regions for which only one effect size was computed (Fig. 7A, red marking). In

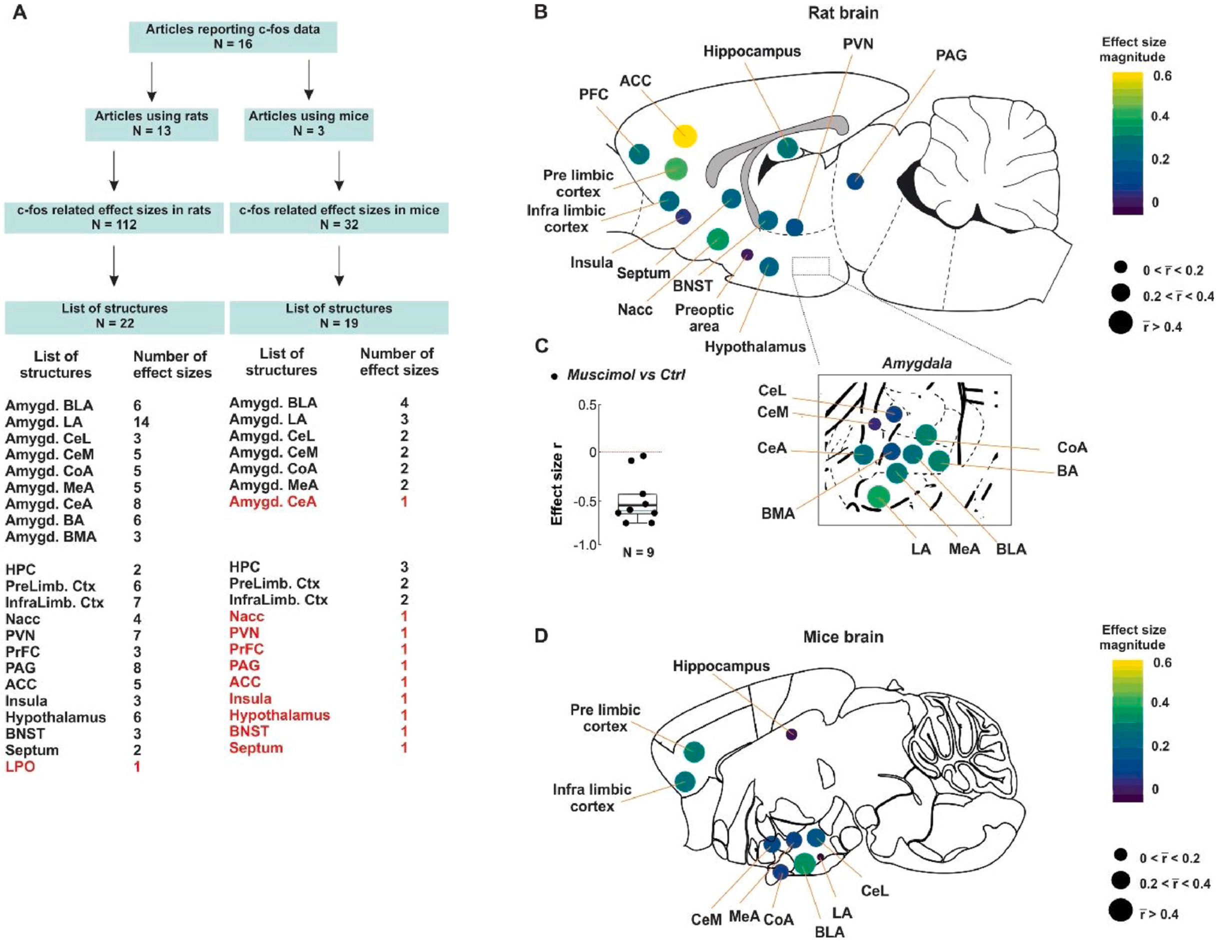


Fig. 7. Brain areas specialized in emotional contagion in the rat and mouse brain. (**A**) Flow chart of studies used to quantify c-fos related effect sizes. Brain structure lists is provided separately for rats and mice. BLA = Basolateral Amygdala; LA = Lateral Amygdala; CeL = Central Lateral Amygdala; CeM = Central Medial Amygdala; CoA = Cortical Amygdala; MeA = Medial Amygdala; CeA = Central Amygdala; BA = Basal Amygdala; BMA = Basomedial Amygdala; HPC = Hippocampus; NAcc = Nucleus Accumben; PVN = Paraventricular Nucleus; PFC = Prefrontal Ctx; PAG = PeriAcqueducal Grey; ACC = Anterior Cingulate Ctx; BNST = Bed of the Stria Terminalis; LPO = Lateral PreOptic area. (**B**) Schematic figures showinga saggital section of the rat brain with effect sizes. (**C**) Boxplot depicting median (black line) and mean (green line) effect sizes computed from comparing emotional contagion levels between groups of mice infused with saline and muscimol. Dots represent individual effect sizes. (**D**) Schematic figure showing a saggital section of the mouse brain with effect sizes. Dots' size and colors inform on effect sizes per structure. Structure with less than 2 effect sizes (red in list) are not reported on the schematics. Brain schematic were taken from (Paxinos and Watson, 1998).

Table 7

Summary of results for c-fos data. Table provides meta-analytics results for different brain structure, separated for rat and mouse. Meta-analytic results are the mean effect size value $\bar{r}$ with the confidence interval (CI), the z score value, heterogeneity value as measured by I^2 and sample size (n). Acronyms can be found in the associated figure's legend.

Species	Brain structure		$\bar{r}$ mean-CI (low-high)	*z*	I^2 %	n
Rat	ACC		0.58 (0.24 ; 0.98)	*3.31*	40.64	5
	PVN		0.08 (-0.31 ; 0.48)	*0.41*	75.79	7
	PFC		0.21 (-0.09 ; 0.53)	1.36	0	3
	Hypothalamus		0.15 (-0.12 ; 0.42)	1.07	0	6
	Hippocampus		0.23 (-0.16 ; 0.64)	1.16	0	2
	Prelimbic Ctx		0.37 (0.07 ; 0.67)	2.43	0	6
	Infralimbic Ctx		0.18 (-0.05 ; 0.42)	1.54	7.07	7
	NAcc		0.31 (-0.05 ; 0.69)	1.67	25.28	4
	PAG		0.04 (-0.29 ; 0.37)	0.24	54.14	8
	Insula		−0.02 (-0.52 ; 0.48)	−0.08	0	3
	BNST		0.17 (-0.11 ; 0.46)	1.16	0	3
	Septum		0.17 (-0.19 ; 0.54)	0.92	0	2
	Amygdala	BLA	0.35 (-0.01 ; 0.70)	1.94	39.77	6
		CeL	0.02 (-0.48 ; 0.52)	0.07	0	3
		CeM	−0.07 (-0.46 ; 0.31]	−0.38	0	5
		CeA	0.21 (0.01 ; 0.40)	2.13	0	8
		CoA	0.26 (-0.15 ; 0.68)	1.21	38.22	5
		LA	0.35(0.01 ; 0.69)	2.01	75.98	14
		BA	0.26 (-0.23 ; 0.77)	1.04	77.88	6
		BMA	0.06 (-0.88 ; 0.99)	0.12	71.06	3
		MeA	0.23 (-0.24 ; 0.72)	0.95	52.75	5
Mouse	Hippocampus		−0.13 (-0.55 ; 0.29)	−0.60	0	3
	Prelimbic Ctx		0.22 (-0.57 ; 1.02)	0.55	56.91	2
	Infralimbic Ctx		0.25 (-0.27 ; 0.77)	0.93	0	2
	Amygdala	BLA	0.30 (-0.01 ; 0.62)	1.88	0	4
		CeL	0.11 (-0.41 ; 0.63)	0.41	0	2
		CeM	0.05 (-0.47 ; 0.56)	0.16	0	2
		CoA	0.01 (-0.56 ; 0.57)	0.01	16.56	2
		LA	−0.17 (-0.60 ; 0.25)	−0.81	0	3
		MeA	0.03 (-0.49 ; 0.54)	0.09	0	2

the case of the ACC, we leveraged a number of studies ($n = 9$) where comparisons in emotional contagion levels were performed between groups of healthy mice and groups of mice where the function of the anterior cingulate cortex had been altered (Fig. 7C). We found that deactivating the ACC in mice strongly reduced emotional contagion ($\bar{r} = 0.58$, CI: [-0.97 to 0.20]), in line with the observation of high c-fos activation levels in the rat ACC during emotional contagion. Regarding c-fos activation pattern, and similar to what was observed in the rat brain, we found that prelimbic and infralimbic cortices are activated during in emotional contagion in mice (Fig. 7D).

While cingulate and limbic cortices were recruited in both rat and mouse brains during emotional contagion, more granular differences emerged within sub-nuclei of the amygdala. In particular, we report that while the BLA is recruited in both species, the LA was activated in rats, but not mice, during emotional contagion.

Altogether, c-fos meta-analytic data suggests a circuit recruited for emotional contagion in rodents that comprises frontal structures (in particular the anterior cingulate, prelimbic and infralimbic cortices) as well as subcortical nuclei (in particular the nucleus accumbens and the amygdala). These observations are in line with the idea that brain areas necessary for the processing of non-social stimuli are also recruited during social cognition (Ruff and Fehr, 2014), and suggest that rodent and human neural substrates of emotional contagion and empathy overlap to some extent (Lamm et al., 2011; Zaki et al., 2016). Recent research suggests that the amygdala and the anterior cingulate cortex are also important for prosocial behavior in rats, i.e., actions that benefit others (Hernandez-Lallement et al., 2016a). That emotional contagion is important for prosocial behavior remains completely unexplored in the field, and future research should explore potential behavioral and neural links between these two processes.

4. Conclusion and limitations

4.1. *Updating current models of emotional contagion*

While a high number of reviews attempting to summarize the literature on emotional contagion in rodents were published in recent years (Keysers and Gazzola, 2016; Meyza et al., 2016; Keum and Shin, 2016; Sivaselvachandran et al., 2016; Mogil, 2012; Lukas and de Jong, 2016; Keum and Shin, 2019), one article in particular went one step further and proposed a classification of experimental approaches used in the field (Panksepp and Panksepp, 2013a). This classification distinguished a variety of phenomenon such as contagion, social analgesia, social buffering, social priming, behavioral matching and social transfer. In the current meta-analysis, we updated and simplified this classification based on our revised inclusion criteria for studies measuring emotional contagion: 'a study measuring a behavioral response associated with (indirectly -in absence of- and directly -in presence of others-) the emotional cues of other individuals'. This means that all the phenomena mentioned above, per our definition, fall under the emotional contagion umbrella. One illustrative example is the case of social buffering, where a distressed animal shows reduced fear when paired with a neutral non-distressed conspecific. In these cases, we considered the observed phenomenon as emotional contagion from an animal in a neutral emotional state to one in a fearful state. This approach allowed us to unify different paradigms, and seemingly diverse approaches on rodent empathy into a single model. Our classification had additional key differences with the classification proposed by Panskepp & Panksepp (Panksepp and Panksepp, 2013a): 1) contagion can occur without the direct presence of an individual (e.g., through a cotton boll soaked with urine of a fearful animal); 2) emotional contagion paradigms consist of three phases: pre-exposure, emotional transfer and measure of emotional contagion; 3) the term *emotional transfer* refers to the point in time in which the emotional state from one individual is contaged to another (measurement time could happen during or after emotional transfer); 4) measurements of emotional contagion had to recruit an emotional observable response; if they failed to do so (such as memory effects), they were not considered direct measurements of emotional contagion but rather secondary processes related to emotional contagion. All the studies included in the current meta-analysis fall under this classification.

4.2. *Limitations*

While we strived to reduce the number of arbitrary decisions that needed to be made (by devising a clear methodology and procedures in the decision process), inevitably, we did encounter difficult choices at different stages of the process. In particular, for each study, we were confronted with interpreting whether the reported data was a direct measure of emotional contagion, or rather a secondary process triggered by emotional contagion. The lack of clear definitions and unity in the field made it challenging in deciding which data was indeed relevant for this meta-analysis. In order to guide our decisions, we elaborated a framework through which each study was pipelined to take a decision on whether the effect size reflected emotional contagion-related data. For instance, research performed on social transmission of taste aversion can be arguably included in the emotional contagion field, since, typically in these paradigms, one animal undergoes an aversive emotion (taste), which is thereafter transmitted to a naïve conspecific through interactions. However, these publications were not included in this meta-analysis due to the fact that the aversive emotion experienced by the demonstrator was often not measured and quantified, nor was the actual transfer of emotion. Similar issues were encountered in studies where emotional contagion was used as a tool, rather than a measure, to study how observing the distress of others affected cognitive abilities later in time, such as memory and learning (Nowak et al., 2013; Ito et al., 2015a). Albeit these are important effects of emotional contagion in other neural processes and behaviors, they are not a direct measurement of emotional contagion, and as such were excluded from the main analysis.

However, we find it important to emphasize the caveats of our approach by pointing out other missing aspects of the emotional contagion literature. For instance, the filters used in this study failed to capture articles on mother-pup interaction and the emotional transfer inherent to such social systems (Moriceau and Sullivan, 2006; Barr et al., 2009). Future meta-analytic work on this topic could increase their search filter range to include such studies and encompass even more variability in rodent emotional contagion.

It should also be noted that our filters might have failed to include articles where similar processes were studied but other wording was used. It is notable that rodent emotional contagion is a controversial topic (Balter, 2011) and several studies have framed their results in terms of stress-related processes instead of emotional contagion (Breitfeld et al., 2015; Zalaquett and Thiessen, 1991; Mackay-Sim and Laing, 1981). While we believe that the high number of effect sizes and studies included in this meta-analysis already allow for careful conclusions to be drawn, future endeavors should carefully increase the granularity of their filters to encompass studies that investigated similar processes under a different framework.

Another limitation of our work is the low number of effect sizes present in some distributions. For instance, the low number of effect sizes reported in females makes it difficult to conclude on the results reported here, that is, that sex does not modulate emotional contagion. Similar parsimony should be used when interpreting effect sizes reported in different strains. For instance, the differences reported between CD-1 and CF-1 mice, two very close strains, are quite surprising. One likely explanation for this (and other) differences might lie in the experimental paradigm used, which differed between strains. These discrepant results suggest that additional, more granular variables should be added to future meta-analysis. For instance, an attempt at classifying experimental paradigms to identify contexts and situations where emotional contagion might be more salient would allow to associate differences in effect sizes to experimental manipulations rather than to species, strains or other parameters.

This meta-analysis revealed that, although, emotional contagion can occur in response to both positive and negative emotions, as already noted by (Panksepp and Panksepp, 2013c), to date nearly all studies investigating emotional contagion in rodents use negative stimuli to trigger emotional transfer, which could be due to the fact that in rodent empathy research negative reinforcers are traditionally used. This observation stresses the need to use positive reinforcers to study the other side of rodent empathy, as already performed in some studies (Willuhn et al., 2014b; Kashtelyan et al., 2014b; Lichtenberg et al., 2018), and more generally in the field of prosocial behavior (Lichtenberg et al., 2018; Márquez et al., 2015; Hernandez-Lallement et al., 2016b, 2020). A promising avenue would lie in studies that directly compare the effects of positive and negative reinforcers, although we acknowledge that developing comparable positive and negative stimulus is a challenge given the higher saliency and reinforcing power of negative stimuli. On the other hand, it is important to consider the possibility, that the under reporting of studies using positive stimuli could be due to lack of effect of this type of stimuli and bias to report null effects.

A final limitation that we encountered was the incomplete reporting of information, namely, the methods section. We noticed that some variables more likely to not be properly reported such as age and number of days that observers and demonstrators were related to each other, with 13 % and 21 % of overall missing values per category respectively. In addition, our quantitative analysis suggested that randomization, blinding and sample size calculations are seldom reported (and/or done) in studies in the field, which overall reduces the results quality.

4.3. Conclusion

Overall, this is the first meta-analysis and systematic review conducted to date on the field of rodent emotional contagion. In this meta-analysis we develop an umbrella definition of emotional contagion that covers a large rage of studies investigating this response. We also developed a classification model that allowed us to unify a range of existing paradigms used to investigate emotional contagion. Within this model we identified key parameters that have a modulatory effect on emotional contagion and that can be used for optimizing the design of future studies in the field. However, we underscore that many differences reported here should be taken cautiously since the lack of effect sizes and major differences in experimental paradigms could still account for effects we report in this meta-analysis. We also identify a range of brain regions that can be used as targets to further our understanding of the neural mechanisms of emotional contagion. Lastly, this meta-analysis also identifies gaps in knowledge and potential research areas of interest.

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References

Allsop, S.A., Wichmann, R., Mills, F., Ba, D., Brown, E.N., Tye, K.M., Allsop, S.A., Wichmann, R., Mills, F., Burgos-robles, A., et al., 2018. Corticoamygdala transfer of socially derived information gates observational learning article corticoamygdala transfer of socially derived information gates observational learning. Cell 1–14.

Anderson, E.E., 1939. The effect of the presence of a second animal upon emotional behavior in the male albino rat. J. Soc. Psychol. 10, 265–268.

Archer, J., 1973. Tests for emotionality in rats and mice a review. Anim. Behav. 21, 205–235.

Armario, A., Ortiz, R., Balasch, J., 1982. Corticoadrenal and Behavioral Response to Open Field in Pairs of Male Rats Either Familiar or Non-Familiar to Each Other, p. 302.

Armario, A., Luna, G., Balasch, J., 1983. The effect of conspecifics on corticoadrenal response of rats to a novel environment. Behav. Neural Biol. 37, 332–337.

Atsak, P., Orre, M., Bakker, P., Cerliani, L., Roozendaal, B., Gazzola, V., Moita, M., Keysers, C., 2011a. Experience modulates vicarious freezing in rats: a model for empathy. PLoS One 6.

Atsak, P., Orre, M., Bakker, P., Cerliani, L., Roozendaal, B., Gazzola, V., Moita, M., Keysers, C., 2011b. Experience modulates vicarious freezing in rats: a model for empathy. PLoS One 6.

Balter, M., 2011. Killjoys' challenge claims of clever animals. Science (80-.) 335, 2011–2012.

Baptista-de-Souza, D., Nunciato, A.C., Pereira, B.C., Fachinni, G., Zaniboni, C.R., Canto-de-Souza, A., 2015. Mice undergoing neuropathic pain induce anxiogenic-like effects and hypernociception in cagemates. Behav. Pharmacol. 26, 664–672.

Barr, G.A., Moriceau, S., Shionoya, K., Muzny, K., Gao, P., Wang, S., Sullivan, R.M., 2009. Transitions in infant learning are modulated by dopamine in the amygdala. Nat. Neurosci. 12, 1367–1369.

Baum, M., 1969a. Extinction of an avoidance response motivated by intense fear-social facilitation of ACtion of response prevention (flooding) in rats. Behav. Res. Ther. 7, 57.

Baum, M., 1969b. Extinction of an avoidance response motivated by intense fear - social facilitation of action of Response Prevention (FLOODING) in rats. Behav. Res. Ther. 7, 57.

Birbaumer, N., Veit, R., Lotze, M., Erb, M., Hermann, C., Grodd, W., Flor, H., 2005. Deficient fear conditioning in psychopathy. Arch. Gen. Psychiatry 62, 799–805.

Blair, R.J.R., 2007. The amygdala and ventromedial prefrontal cortex in morality and psychopathy. Trends Cogn. Sci. 11, 387–392.

Blair, R.J.R., Budhani, S., Colledge, E., Scott, S., 2005. Deafness to fear in boys with psychopathic tendencies. J. Child Psychol. Psychiatry Allied Discip. 46, 327–336.

Boivin, G.P., Bottomley, M.A., Grobe, N., 2016. Responses of male C57BL/6N mice to observing the euthanasia of other mice. J. Am. Assoc. Lab. Anim. Sci. 55, 406–411.

Bowen, M.T., Kevin, R.C., May, M., Staples, L.G., Hunt, G.E., McGregor, I.S., 2013. Defensive aggregation (Huddling) in Rattus norvegicus toward predator odor: individual differences, social buffering effects and neural correlates. PLoS One 8.

Bredy, T.W., Barad, M., 2009. Social modulation of associative fear learning by pheromone communication. Learn. Mem. 16, 12–18.

Breitfeld, T., Bruning, J.E.A., Inagaki, H., Takeuchi, Y., Kiyokawa, Y., Fendt, M., 2015. Temporary inactivation of the anterior part of the bed nucleus of the stria terminalis blocks alarm pheromone-induced defensive behavior in rats. Front. Neurosci. 9, 1–8.

Brill-Maoz, N., Maroun, M., 2016. Extinction of fear is facilitated by social presence: synergism with prefrontal oxytocin. Psychoneuroendocrinology 66, 75–81.

Bruchey, A.K., Jones, C.E., Monfils, M.-H., 2010. Fear conditioning by-proxy: social transmission of fear during memory retrieval. Behav. Brain Res. 214, 80–84.

Carneiro de Oliveira, P.E., Zaniboni, C.R., Carmona, I.M., Fonseca, A.R., Canto-de-Souza, A., 2017. Preliminary behavioral assessment of cagemates living with conspecifics submitted to chronic restraint stress in mice. Neurosci. Lett. 657, 204–210.

Carrillo, M., Migliorati, F., Bruls, R., Han, Y., Heinemans, M., Pruis, I., Gazzola, V., Keysers, C., 2015. Repeated witnessing of conspecifics in pain: effects on emotional contagion. PLoS One 10, 1–11.

Chang, D.-J., Debiec, J., 2016. Neural correlates of the mother-to-infant social transmission of fear. J. Neurosci. Res. 94, 526–534.

Chen, Q.L., Panksepp, J.B., Lahvis, G.P., 2009. Empathy is moderated by genetic background in mice. PLoS One 4, 1–14.

Chen, J., Li, C.-L., Wang, Y., Yang, Y., Li, Z., Lü, Y.-F., 2017. The locus coeruleus–Norepinephrine system mediates empathy for pain through selective up-regulation of P2X3 receptor in dorsal root ganglia in rats. Front. Neural Circuits 11, 1–15.

Choi, J., Jeong, Y., 2017. Elevated emotional contagion in a mouse model of Alzheimer's disease is associated with increased synchronization in the insula and amygdala. Nat. Publ. Gr. 1–9.

Church, R.M., 1959. Emotional reactions of rats to the pain of others. J. Comp. Physiol. Psychol. 52, 132–134.

Colnaghi, L., Clemenza, K., Groleau, S.E., Weiss, S., Snyder, A.M., Lopez-Rosas, M., Levine, A.A., 2016. Social involvement modulates the response to novel and adverse life events in mice. PLoS One 11, e0163077.

Daniel, W.J., 1942. Cooperative problem solving in rats. J. Comp. Psychol. 34, 361–368.

Daniel, W.J., 1943. Higher Order Cooperative Problem Solving in Rats, pp. 297–305.

Davitz, J.R., Mason, D.J., 1955. Socially facilitated reduction of a fear response in rats. J. Comp. Physiol. Psychol. 48, 149–151.

Dawel, A., O'Kearney, R., McKone, E., Palermo, R., 2012. Not just fear and sadness: meta-analytic evidence of pervasive emotion recognition deficits for facial and vocal expressions in psychopathy. Neurosci. Biobehav. Rev. 36, 2288–2304.

De Waal, F.B.M., Preston, S.D., 2017. Mammalian empathy: behavioural manifestations and neural basis. Nat. Rev. Neurosci. 18, 498–509.

Debiec, J., Sullivan, R.M., 2014. Intergenerational transmission of emotional trauma through amygdala-dependent mother-to-infant transfer of specific fear. Proc. Natl. Acad. Sci. U. S. A. 111, 12222–12227.

Dolan, M., Fullam, R., 2006. Face affect recognition deficits in personality-disordered offenders: association with psychopathy. Psychol. Med. (Paris) 36, 1563–1569.

Fiore, M., Ingiosi, D., Carito, V., Huzard, D., Laviola, G., Macrì, S., Zoratto, F., 2017. Low empathy-like behaviour in male mice associates with impaired sociability, emotional memory, physiological stress reactivity and variations in neurobiological regulations. PLoS One 12, e0188907.

Fuzzo, F., Matsumoto, J., Kiyokawa, Y., Takeuchi, Y., Ono, T., Nishijo, H., 2015. Social buffering suppresses fear-associated activation of the lateral amygdala in male rats: behavioral and neurophysiological evidence. Front. Neurosci. 9, 1–8.

Gioiosa, L., Chiarotti, F., Alleva, E., Laviola, G., 2009. A trouble shared is a trouble halved: social context and status affect pain in mouse dyads. PLoS One 4.

Gonzalez-Liencres, C., Juckel, G., Tas, C., Friebe, A., Bruene, M., 2014a. Emotional contagion in mice: the role of familiarity. Behav. Brain Res. 263, 16–21.

Gonzalez-Liencres, C., Juckel, G., Tas, C., Friebe, A., Brüne, M., 2014b. Emotional contagion in mice: the role of familiarity. Behav. Brain Res. 263, 16–21.

Gonzalez-Liencres, C., Juckel, G., Esslinger, M., Wachholz, S., Manitz, M.-P., Brüne, M., Friebe, A., 2016. Emotional contagion is not altered in mice prenatally exposed to poly (I:C) on gestational day 9. Front. Behav. Neurosci. 10.

Greene, J.T., 1969. Altruistic behavior in the albino rat. Psychon. Sci. 14, 47–48.

Gurevitch, J., Koricheva, J., Nakagawa, S., Stewart, G., 2018. Meta-analysis and the science of research synthesis. Nature 555, 175–182.

Guzmán, Y.F., Tronson, N.C., Guedea, A., Huh, K.H., Gao, C., Radulovic, J., 2009. Social modeling of conditioned fear in mice by non-fearful conspecifics. Behav. Brain Res. 201, 173–178.

Hachiga, Yosuke, Schwartz, Lindsay, Silberberg, Alan, Kearns, David, Gomez, Maria, Slotnick, Burton, 2018. Does a rat free trapped rat due to empathy or for sociality? Journal experimental animal behaviour 110 (2), 267–274. https://doi.org/10.1002/jeab.464.

Hammerschmidt, K., Radyushkin, K., Ehrenreich, H., Fischer, J., 2009. Female mice respond to male ultrasonic `songs' with approach behaviour. Biol. Lett. 5, 589–592.

Han, Y., Bruls, R., Soyman, E., Thomas, R., Pentaraki, V., Jelinek, N., Heinemans, M., Bassez, I., Verschooren, S., Pruis, I., et al., 2019a. Bidirectional cingulate-dependent danger information transfer across rats. PLoS Biol. 17 (12), e3000524. https://doi.org/10.1371/journal.pbio.3000524.

Han, Y., Sichterman, B., Carrillo, M., Gazzola, V., Keysers, C., 2019b. Similar levels of emotional contagion in male and female rats. Sci. Rep., 857094

Harb, R., Taylor, J.R., 2015. The fragrant power of collective fear. PLoS One 10, e0123908.

Hedges, L., Olkin, I., 1985. Statistical methods for meta-analysis. Stat. Methods Meta-Analysis 6, 107–128.

Hernandez-Lallement, J., van Wingerden, M., Schäble, S., Kalenscher, T., 2016a. Basolateral amygdala lesions abolish mutual reward preferences in rats. Neurobiol. Learn. Mem. 127, 1–9.

Hernandez-Lallement, J., van Wingerden, M., Schäble, S., Kalenscher, T., 2016b. A social reinforcement learning hypothesis for mutual reward preference in rats. Curr. Top. Behav. Neurosci. 289–320.

Hernandez-Lallement, J., Attah, A.T., Soyman, E., Pinhal, C.M., Gazzola, V., Keysers, C., 2020. Harm to others acts as a negative reinforcer in rats. Curr. Biol. 30, 949–961 e7.

Higgins, J.P.T., Thompson, S.G., 2002. Quantifying heterogeneity in a meta-analysis. Stat. Methods Meta-Analysis 1558, 1539–1558.

Higgins, J.P.T., Thompson, S.G., Deeks, J.J., Altman, D.G., 2003. Measuring inconsistency in meta-analyses. BMJ 327, 557–560.

Hishimura, Y., 2015. Interactions with conspecific attenuate conditioned taste aversions in mice. Behav. Processes 111, 34–36.

Hodges, T.E., Green, M.R., Simone, J.J., McCormick, C.M., 2014. Effects of social context on endocrine function and Zif268 expression in response to an acute stressor in adolescent and adult rats. Int. J. Dev. Neurosci. 35, 25–34.

Hong, E.H., Choi, J.S., 2018. Observational threat conditioning is induced by circa-strike activity burst but not freezing and requires visual attention. Behav. Brain Res. 353, 161–167.

Hunter, A.S., 2014. The effects of social housing on extinction of fear conditioning in rapid eye movement sleep-deprived rats. Exp. Brain Res. 232, 1459–1467. Available at: https://pubmed.ncbi.nlm.nih.gov/24449010/ [Accessed 28 August 2020].

Inagaki, H., Ushida, T., 2017. Changes in acoustic startle reflex in rats induced by playback of 22-kHz calls. Physiol. Behav. 169, 189–194.

Ishii, A., Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2016. Social buffering ameliorates conditioned fear responses in female rats. Horm. Behav. 81, 53–58.

Ito, W., Erisir, A., Morozov, A., 2015a. Observation of distressed conspecific as a model of emotional trauma generates silent synapses in the prefrontal-amygdala pathway and enhances fear learning, but ketamine abolishes those effects. Neuropsychopharmacology 40, 1–32.

Janezic, E.M., Uppalapati, S., Nagl, S., Contreras, M., French, E.D., Fellous, J.-M., 2016. Beneficial effects of chronic oxytocin administration and social co-housing in a rodent model of post-traumatic stress disorder. Behav. Pharmacol. 27, 704–717.

Jeon, D., Kim, S., Chetana, M., Jo, D., Ruley, H.E., Lin, S.-Y., Rabah, D., Kinet, J.-P., Shin, H.-S., 2010. Observational fear learning involves affective pain system and Cav1.2 Ca2+ channels in ACC. Nat. Neurosci. 13, 482–488.

Jones, C.E., Monfils, M.-H., 2016a. Dominance status predicts social fear transmission in laboratory rats. Anim. Cogn. 19, 1051–1069.

Jones, C.E., Monfils, M.-H., 2016b. Post-retrieval extinction in adolescence prevents return of juvenile fear. Learn. Mem. 23, 567–575.

Jones, C.E., Riha, P.D., Gore, A.C., Monfils, M.-H., 2014. Social transmission of Pavlovian fear: fear-conditioning by-proxy in related female rats. Anim. Cogn. 17, 827–834.

Jung, S., Seo, J.S., Kim, B.S., Lee, D., Jung, K.-H., Chu, K., Lee, S.K., Jeon, D., 2013. Social deficits in the AY-9944 mouse model of atypical absence epilepsy. Behav. Brain Res. 236, 23–29.

Kashtelyan, V., Lichtenberg, N.T., Chen, M.L., Cheer, J.F., Roesch, M.R., 2014a. Observation of reward delivery to a conspecific modulates dopamine release in ventral striatum. Curr. Biol. 24, 2564–2568.

Kashtelyan, V., Lichtenberg, N.T., Chen, M.L., Cheer, J.F., Roesch, M.R., 2014b. Observation of reward delivery to a conspecific modulates dopamine release in ventral striatum. Curr. Biol. 24, 2564–2568.

Kavaliers, M., Colwell, D.D., Choleris, E., 2001a. NMDA-mediated social learning of fear-induced conditioned analgesia to biting flies. Neuroreport 12, 663–667.

Kavaliers, M., Choleris, E., Colwell, D.D., 2001b. Learning from others to cope with biting flies: social learning of fear-induced conditioned analgesia and active avoidance. Behav. Neurosci. 115, 661–674.

Kavaliers, M., Colwell, D.D., Choleris, E., 2005. Kinship, familiarity and social status modulate social learning about "micropredators" (biting flies) in deer mice. Behav. Ecol. Sociobiol. 58, 60–71.

Keum, S., Shin, H.-S., 2016. Rodent models for studying empathy. Neurobiol. Learn. Mem. 135, 22–26.

Keum, S., Shin, H.S., 2019. Neural basis of observational fear learning: a potential model of affective empathy. Neuron 104, 78–86.

Keum, S., Park, J., Kim, A., Park, J., Kim, K.K., Jeong, J., Shin, H.S., 2016. Variability in empathic fear response among 11 inbred strains of mice. Genes Brain Behav. 15, 231–242.

Keum, S., Kim, A., Shin, J.J., Kim, J.H., Park, J., Shin, H.S., 2018. A missense variant at the Nrxn3 locus enhances empathy fear in the mouse. Neuron 98, 588–601 e5.

Keysers, C., Gazzola, V., 2016. A plea for cross-species social neuroscience. Curr. Top. Behav. Neurosci.

Kikusui, T., Ishio, Y., Nagasawa, M., Mogil, J.S., Mogi, K., 2016. Early weaning impairs a social contagion of pain-related stretching behavior in mice. Dev. Psychobiol. 58, 1101–1107.

Kim, E.J., Kim, E.S., Covey, E., Kim, J.J., 2010. Social transmission of fear in rats: the role of 22-kHz ultrasonic distress vocalization. PLoS One 5, e15077.

Kim, S., Matyas, F., Lee, S., Acsady, L., Shin, H.-S., 2012. Lateralization of observational fear learning at the cortical but not thalamic level in mice. Proc. Natl. Acad. Sci. U. S. A. 109, 15497–15501.

Kim, B.S., Lee, J., Bang, M., Seo, B.A., Khalid, A., Jung, M.W., Jeon, D., 2014. Differential regulation of observational fear and neural oscillations by serotonin and dopamine in the mouse anterior cingulate cortex. Psychopharmacology (Berl.) 231, 4371–4381.

Kiyokawa, Y., Takeuchi, Y., 2017. Social buffering ameliorates conditioned fear responses in the presence of an auditory conditioned stimulus. Physiol. Behav. 168, 34–40.

Kiyokawa, Y., Kikusui, T., Takeuchi, Y., Mori, Y., 2004a. Partner's stress status influences social buffering effects in rats. Behav. Neurosci. 118, 798–804.

Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2007. Two types of social buffering differentially mitigate conditioned fear responses. Eur. J. Neurosci. 26, 3606–3613.

Kiyokawa, Y., Takeuchi, Y., Nishihara, M., Mori, Y., 2009. Main olfactory system mediates social buffering of conditioned fear responses in male rats. Eur. J. Neurosci. 29, 777–785.

Kiyokawa, Y., Wakabayashi, Y., Takeuchi, Y., Mori, Y., 2012. The neural pathway underlying social buffering of conditioned fear responses in male rats. Eur. J. Neurosci. 36, 3429–3437.

Kiyokawa, Y., Kodama, Y., Takeuchi, Y., Mori, Y., 2013. Physical interaction is not necessary for the induction of housing-type social buffering of conditioned hyperthermia in male rats. Behav. Brain Res. 256, 414–419.

Kiyokawa, Y., Honda, A., Takeuchi, Y., Mori, Y., 2014a. A familiar conspecific is more effective than an unfamiliar conspecific for social buffering of conditioned fear responses in male rats. Behav. Brain Res. 267, 189–193.

Kiyokawa, Y., Hiroshima, S., Takeuchi, Y., Mod, Y., 2014b. Social buffering reduces male rats' behavioral and corticosterone responses to a conditioned stimulus. Horm. Behav. 65, 114–118.

Kiyokawa, Y., Ishida, A., Takeuchi, Y., Mori, Y., 2016. Sustained housing-type social buffering following social housing in male rats. Physiol. Behav. 158, 85–89.

Kiyokawa, Y., Kawai, K., Takeuchi, Y., 2018. The benefits of social buffering are maintained regardless of the stress level of the subject rat and enhanced by more conspecifics. Physiol. Behav. 194, 177–183.

Knapska, E., Nikolaev, E., Boguszewski, P., Walasek, G., Blaszczyk, J., Kaczmarek, L., Werka, T., 2006a. Between-subject transfer of emotional information evokes specific pattern of amygdala activation. Proc. Natl. Acad. Sci. U. S. A. 103, 3858–3862.

Knapska, E., Mikosz, M., Werka, T., Maren, S., 2010. Social modulation of learning in rats. Learn. Mem. 17, 35–42.

Kodama, Y., Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2011. Twelve hours is sufficient for social buffering of conditioned hyperthermia. Physiol. Behav. 102, 188–192.

Korman, M., Loeb, J., 1961. Effects of the presence of another animal during acquisition and extinction upon the strength of a fear response. J. Comp. Physiol. Psychol. 54, 158–161.

Krebs, D., 1971. Infrahuman altruism. Psychol. Bull. 76, 411–414.

Lamm, C., Decety, J., Singer, T., 2011. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. Neuroimage 54, 2492–2502.

Langford, D.J., 2006. Social modulation of pain as evidence for empathy in mice. Science (80-.) 312, 1967–1970.

Langford, D.J., Crager, S.E., Shehzad, Z., Smith, S.B., Sotocinal, S.G., Levenstadt, J.S., Chanda, M.L., Levitin, D.J., Mogil, J.S., 2006. Social modulation of pain as evidence for empathy in mice. Science (80-.) 312, 1967–1970.

Langford, D.J., Tuttle, A.H., Brown, K., Deschenes, S., Fischer, D.B., Mutso, A., Root, K.C., Sotocinal, S.G., Stern, M.A., Mogil, J.S., et al., 2010a. Social approach to pain in laboratory mice. Soc. Neurosci. 5, 163–170.

Langford, D.J., Tuttle, A.H., Brown, K., Deschenes, S., Fischer, D.B., Mutso, A., Root, K.C., Sotocinal, S.G., Stern, M.A., Mogil, J.S., et al., 2010b. Social approach to pain in laboratory mice. Soc. Neurosci. 5, 163–170.

Langford, D.J., Tuttle, A.H., Briscoe, C., Harvey-Lewis, C., Baran, I., Gleeson, P., Fischer, D.B., Buonora, M., Sternberg, W.F., Mogil, J.S., 2011. Varying perceived social threat modulates pain behavior in male mice. J. Pain 12, 125–132.

Latané, B., 1969. Gregariousness and fear in laboratory rats. J. Exp. Soc. Psychol. 5, 61–69.

Lau, J., Ioannidis, J.P.A., Terrin, N., Schmid, C.H., Olkin, I., 2006. The case of the misleading funnel plot. BMC 33, 597–600.

Lavery, J.J., Foley, P.J., 1963. Altruism or arousal in rat. Science (80-.) 140, 172.

Lee, H., Noh, J., 2015. Social exclusion intensifies anxiety-like behavior in adolescent rats. Behav. Brain Res. 284, 112–117.

Lee, H., Noh, J., 2016. Pair exposure with conspecific during fear conditioning induces the link between freezing and passive avoidance behaviors in rats. Neurosci. Res. 108, 40–45.

Leenaars, M., Hooijmans, C.R., van Veggel, N., ter Riet, G., Leeflang, M., Hooft, L., van der Wilt, G.J., Tillema, A., Ritskes-Hoitinga, M., 2012. A step-by-step guide to systematically identify all relevant animal studies. Lab. Anim. 46, 24–31.

Leichsenring, F., 2001. Comparative effects of short-term psychodynamic psychotherapy and cognitive-behavioral therapy in depression: a meta-analytic approach. Clin. Psychol. Rev. 21, 401–419.

Li, Z., Lu, Y.-F., Li, C.-L., Wang, Y., Sun, W., He, T., Chen, X.-F., Wang, X.-L., Chen, J., 2014a. Social interaction with a cagemate in pain facilitates subsequent spinal nociception via activation of the medial prefrontal cortex in rats. Pain 155, 1253–1261.

Li, Z., Lu, Y.F., Li, C.L., Wang, Y., Sun, W., He, T., Chen, X.F., Wang, X.L., Chen, J., 2014b. Social interaction with a cagemate in pain facilitates subsequent spinal nociception via activation of the medial prefrontal cortex in rats. Pain 155, 1253–1261.

Li, C.-L., Wang, R.-R., Wei, N., Chen, J., Yang, Y., Wang, X.-L., Luo, W.-J., Yu, Y., Wang, Y., Geng, K.-W., et al., 2018. Validating rat model of empathy for pain: effects of pain expressions in social partners. Front. Behav. Neurosci. 12, 1–16.

Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gøtzsche, P.C., Ioannidis, J.P.A., Clarke, M., Devereaux, P.J., Kleijnen, J., Moher, D., 2009. The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate healthcare interventions: explanation and elaboration. BMJ 339.

Lichtenberg, N.T., Lee, B., Kashtelyan, V., Chappa, B.S., Girma, H.T., Green, E.A., Kantor, S., Lagowala, D.A., Myers, M.A., Potemri, D., et al., 2018. Rat behavior and dopamine release are modulated by conspecific distress. Elife 7, 1–24.

Lipsey, M., Wilson, D.B., 2001. Pratical Meta-Analysis. S. Publications.

Liu, H., Yuan, T.-F., 2016. Physical interaction is required in social buffering induced by a familiar conspecific. Sci. Rep. 6, 39788.

Livia Terranova, M., Cirulli, F., Laviola, G., 1999. Behavioral and hormonal effects of partner familiarity in periadolescent rat pairs upon novelty exposure. Psychoneuroendocrinology 24, 639–656. Available at: https://pubmed.ncbi.nlm.nih.gov/10399773/ [Accessed 28 August 2020].

Lu, Y.F., Ren, B., Ling, B.F., Zhang, J., Xu, C., Li, Z., 2018. Social interaction with a cagemate in pain increases allogrooming and induces pain hypersensitivity in the observer rats. Neurosci. Lett. 662, 385–388. Available at: https://pubmed.ncbi.nlm.nih.gov/29102786/ [Accessed 28 August 2020].

Lukas, M., de Jong, T., 2016. Conspecific interactions in adult laboratory rodents friends or foes. Neurosci. Biobehav. Rev. 30, 3–24.

Lukkes, J.L., Mokin, M.V., Scholl, J.L., Forster, G.L., 2009. Adult rats exposed to early-life social isolation exhibit increased anxiety and conditioned fear behavior, and altered hormonal stress responses. Horm. Behav. 55, 248–256.

Mackay-Sim, A., Laing, D.G., 1981. Rat's responses to blood and body odors of stressed and non-stressed conspecifics. Physiol. Behav. 27, 503–510.

Macrì, S., Martinelli, A., Zoratto, F., Laviola, G., Glennon, J.C., Sbriccoli, M., 2018. Intranasal oxytocin administration promotes emotional contagion and reduces aggression in a mouse model of callousness. Neuropharmacology 143, 250–267.

Márquez, C., Rennie, S.M., Costa, D.F., Moita, M.A., 2015. Prosocial choice in rats depends on food-seeking behavior displayed by recipients. Curr. Biol. 25, 1736–1745.

Marsch, A.A., Blair, R.J.R., 2008. Deficits in facial affect recognition among antisocial populations. Neurosci. Biobehav. Rev. 32, 454–465.

Marsh, A.A., Blair, R.J.R., 2008. Deficits in facial affect recognition among antisocial populations: a meta-analysis. Neurosci. Biobehav. Rev. 32, 454–465.

Martin, L.J., Hathaway, G., Isbester, K., Mirali, S., Acland, E.L., Niederstrasser, N., Slepian, P.M., Trost, Z., Bartz, J.A., Sapolsky, R.M., et al., 2015. Reducing social stress elicits emotional contagion of pain in mouse and human strangers. Curr. Biol. 25, 326–332.

Masuda, A., Aou, S., 2009. Social transmission of avoidance behavior under situational change in learned and unlearned rats. PLoS One 4.

Masuda, A., Narikiyo, K., Someya, N., Aou, S., 2013. Multisensory interaction mediates the social transmission of avoidance in rats: dissociation from social transmission of fear. Behav. Brain Res. 252, 334–338.

Meffert, H., Gazzola, V., Den Boer, J.A., Bartels, A.A.J., Keysers, C., 2013. Reduced spontaneous but relatively normal deliberate vicarious representations in psychopathy. Brain 136, 2550–2562.

Meyza, K.Z., Bartal Ben-Ami, I., Monfils, M.H., Panksepp, J.B., Knapska, E., 2016. The roots of empathy: through the lens of rodent models. Neurosci. Biobehav. Rev.

Meyza, K., Nikolaev, T., Kondrakiewicz, K., Blanchard, D.C., Blanchard, R.J., Knapska, E., 2015. Neuronal correlates of asocial behavior in a BTBR T+Itpr3tf/J mouse model of autism. Front. Behav. Neurosci. 9, 1–13. https://doi.org/10.3389/fnbeh.2015.00199.

Mikami, K., Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2016. Social buffering enhances extinction of conditioned fear responses in male rats. Physiol. Behav. 163, 123–128.

Mogil, J.S., 2012. The surprising empathic abilities of rodents. Trends Cogn. Sci. 16, 143–144.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., 2009. Preferred reporting items for systematic reviews and meta-analyses. Ann. Intern. Med. 151, 264–269.

Moher, D., Shamseer, L., Clarke, M., Ghersi, D., Liberati, A., Petticrew, M., Shekelle, P., Stewart, L.A., Altman, D.G., Booth, A., et al., 2015. Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015 statement. Syst. Rev. 4, 148–160.

Moriceau, S., Sullivan, R.M., 2006. Maternal presence serves as a switch between learning fear and attraction in infancy. Nat. Neurosci. 9, 1004–1006.

Moul, C., Killcross, S., Dadds, M.R., 2012. A model of differential amygdala activation in psychopathy. Psychol. Rev. 119, 789–806.

Mulvihill, K.G., Brudzynski, S.M., 2018. Non-pharmacological induction of rat 50 kHz ultrasonic vocalization: social and non-social contexts differentially induce 50 kHz call subtypes. Physiol. Behav. 196, 200–207.

Muñoz, L.C., 2009. Callous-unemotional traits are related to combined deficits in recognizing afraid faces and body poses. J. Am. Acad. Child Adolesc. Psychiatry 48, 554–562.

Muyama, H., Kiyokawa, Y., Inagaki, H., Takeuchi, Y., Mori, Y., 2016. Alarm pheromone does not modulate 22-kHz calls in male rats. Physiol. Behav. 156, 59–63.

Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance : a practical guide for biologists. Biol. Rev. 82, 591–605.

Nakamura, K., Ishii, A., Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2016. The strain of an accompanying conspecific affects the efficacy of social buffering in male rats. Horm. Behav. 82, 72–77.

Nakashima, S.F., Ukezono, M., Nishida, H., Sudo, R., Takano, Y., 2015. Receiving of emotional signal of pain from conspecifics in laboratory rats. R. Soc. Open Sci. 2, 140381–140381.

Nakayasu, T., Kato, K., 2011. Is full physical contact necessary for buffering effects of pair housing on social stress in rats? Behav. Processes 86, 230–235.

Nowak, A., Werka, T., Knapska, E., 2013. Social modulation in extinction of aversive memories. Behav. Brain Res. 238, 200–205.

Ouda, L., Jílek, M., Syka, J., 2016. Expression of c-Fos in rat auditory and limbic systems following 22-kHz calls. Behav. Brain Res. 308, 196–204.

Panksepp, J., 2011. The basic emotional circuits of mammalian brains: do animals have affective lives? Neurosci. Biobehav. Rev. 35, 1791–1804.

Panksepp, J.B., Lahvis, G.P., 2016. Differential influence of social versus isolate housing on vicarious fear learning in adolescent mice. Behav. Neurosci. 130, 206–211.

Panksepp, J., Panksepp, J.B., 2013a. Toward a cross-species understanding of empathy. Trends Neurosci. 36, 489–496.

Panksepp, J., Panksepp, J.B., 2013b. Toward a cross-species understanding of empathy. Trends Neurosci. 36, 489–496.

Panksepp, J., Panksepp, J.B., 2013c. Toward a cross-species understanding of empathy. Trends Neurosci. 36, 489–496.

Parsana, A.J., Li, N., Brown, T.H., 2012a. Positive and negative ultrasonic social signals elicit opposing firing patterns in rat amygdala. Behav. Brain Res. 226, 77–86.

Parsana, A.J., Moran, E.E., Brown, T.H., 2012b. Rats learn to freeze to 22-kHz ultrasonic vocalizations through autoconditioning. Behav. Brain Res. 232, 395–399.

Paxinos, G., Watson, C., 1998. The Rat Brain Atlas in Stereotaxic Coordinates.

Pisansky, M.T., Hanson, L.R., Gottesman, I.I., Gewirtz, J.C., 2017. Oxytocin enhances observational fear in mice. Nat. Commun. 1–11.

Pitcher, M.H., Gonzalez-Cano, R., Vincent, K., Lehmann, M., Cobos, E.J., Coderre, T.J., Baeyens, J.M., Cervero, F., 2017. Mild social stress in mice produces opioid-mediated analgesia in visceral but not somatic pain states. J. Pain 18, 716–725.

Preston, S.D., De Waal, F.B.M., 2002. Empathy: Its Ultimate and Proximate Bases, pp. 1–71.

Rice, G.E., Gainer, P., 1962. “Altruism” in the albino rat. J. Comp. Physiol. Psychol. 55, 123–125.

Riess, D., 1972. Vicarious conditioned acceleration: successful observational learning of an aversive Pavlovian stimulus contingency. J. Exp. Anal. Behav. 18, 181–186.

Rivara, S., Montano, N., Carnevali, L., Ferrari, P.F., Statello, R., Sgoifo, A., Vacondio, F., Coudé, G., 2017. Social stress contagion in rats: behavioural, autonomic and neuroendocrine correlates. Psychoneuroendocrinology 82, 155–163.

Rogers-Carter, M.M., Djerdjaj, A., Culp, A.R., Elbaz, J.A., Christianson, J.P., 2018. Familiarity modulates social approach toward stressed conspecifics in female rats. PLoS One 13, 1–12.

Ruff, C.C., Fehr, E., 2014. The neurobiology of rewards and values in social decision making. Nat. Rev. Neurosci. 15, 549–562.

Sadananda, M., Wöhr, M., Schwarting, R.K.W., 2008. Playback of 22-kHz and 50-kHz ultrasonic vocalizations induces differential c-fos expression in rat brain. Neurosci. Lett. 435, 17–23.

Saito, Y., Yuki, S., Seki, Y., Kagawa, H., Okanoya, K., 2016. Cognitive bias in rats evoked by ultrasonic vocalizations suggests emotional contagion. Behav. Processes 132, 5–11.

Sakaguchi, T., Iwasaki, S., Okada, M., Okamoto, K., Ikegaya, Y., 2018. Ethanol facilitates socially evoked memory recall in mice by recruiting pain-sensitive anterior cingulate cortical neurons. Nat. Commun. 9.

SALES, G.D., 1991. The effect of 22 Khz calls and artificial 38 Khz signals on activity in rats. Behav. Processes 24, 83–93.

Sanders, J., Mayford, M., Jeste, D., 2013. Empathic fear responses in mice are triggered by recognition of a shared experience. PLoS One 8, e74609.

Schwartz, L.P., Silberberg, A., Casey, A.H., Kearns, D.N., Slotnick, B., 2016. Does a rat release a soaked conspecific due to empathy? Anim. Cogn. 20 (2), 299–308.

Seffer, D., Schwarting, R.K.W., Wöhr, M., 2014. Pro-social ultrasonic communication in rats: insights from playback studies. J. Neurosci. Methods 234, 73–81.

Silberberg, A., Allouch, C., Sandfort, S., Kearns, D., Karpel, H., Slotnick, B., 2014. Desire for social contact, not empathy, may explain ``rescue{''} behavior in rats. Anim. Cogn. 17, 609–618.

Sivaselvachandran, S., Acland, E.L., Abdallah, S., Martin, L.J., 2016. Behavioral and mechanistic insight into rodent empathy. Neurosci. Biobehav. Rev. 1–8.

Smith, M.L., Hostetler, C.M., Heinricher, M.M., Ryabinin, A.E., 2016. Social transfer of pain in mice. Sci. Adv. 2 e1600855–e1600855.

Smith, M.L., Walcott, A.T., Heinricher, M.M., Ryabinin, A.E., 2017. Anterior cingulate cortex contributes to alcohol withdrawal- induced and socially transferred hyperalgesia. Eneuro 4. ENEURO.0087-17.2017.

Sterley, T.L., Baimoukhametova, D., Füzesi, T., Zurek, A.A., Daviu, N., Rasiah, N.P., Rosenegger, D., Bains, J.S., 2018. Social transmission and buffering of synaptic changes after stress. Nat. Neurosci. 21, 393–403.

Suzuki, H., Lucas, L.R., 2015. Neurochemical correlates of accumbal dopamine D-2 and amygdaloid 5-HT1B receptor densities on observational learning of aggression. Cogn. Affect. Behav. Neurosci. 15, 460–474.

Takahashi, Y., Kiyokawa, Y., Kodama, Y., Arata, S., Takeuchi, Y., Mori, Y., 2013. Olfactory signals mediate social buffering of conditioned fear responses in male rats. Behav. Brain Res. 240, 46–51.

Twining, R.C., Vantrease, J.E., Love, S., Padival, M., Rosenkranz, J.A., 2017. An intra-amygdala circuit specifically regulates social fear learning. Nat. Neurosci. 20, 459–469.

Ueno, H., Suemitsu, S., Murakami, S., Kitamura, N., Wani, K., Okamoto, M., Matsumoto, Y., Aoki, S., Ishihara, T., 2018. Empathic behavior according to the state of others in mice. Brain Behav. 8.

Uno, T., Greer, S.E., Goates, L., 1973. Observational facilitation of response prevention. Behav. Res. Ther. 11, 207–212.

Vasconcelos, M., Hollis, K., Nowbahari, E., Kacelnik, A., 2012. Pro-sociality without empathy. Biol. Lett. 8, 910–912.

Watanabe, S., 2011. Empathy and reversed empathy of stress in mice. PLoS One 6. Available at: https://pubmed.ncbi.nlm.nih.gov/21853115/ [Accessed 28 August 2020].

Watanabe, S., 2012. Distress of mice induces approach behavior but has an aversive property for conspecifics. Behav. Processes 90, 167–173.

Watanabe, S., 2015. Social factors modulate restraint stress induced hyperthermia in mice. Brain Res. 1624, 134–139.

West, S.A., Griffin, A.S., Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415–432.

White, D.J., Galef, B.G., 1998. Social influence on avoidance of dangerous stimuli by rats. Anim. Learn. Behav. 26, 433–438.

Willadsen, M., Seffer, D., Schwarting, R.K.W., Wöhr, M., 2014. Rodent ultrasonic communication: male prosocial 50-kHz ultrasonic vocalizations elicit social approach behavior in female rats (Rattus norvegicus). J. Comp. Psychol. 128, 56–64.

Willuhn, I., Tose, a., Wanat, M.J., Hart, a.S., Hollon, N.G., Phillips, P.E.M., Schwarting, R. K.W., Wohr, M., 2014b. Phasic dopamine release in the nucleus accumbens in response to pro-social 50 kHz ultrasonic vocalizations in rats. J. Neurosci. 34, 10616–10623.

Wohr, M., Schwarting, R.K.W., 2007. Ultrasonic communication in rats: can playback of 50-kHz calls induce approach behavior? PLoS One 2, e1365.

Wöhr, M., Schwarting, R.K.W., 2007. Ultrasonic communication in rats: Can playback of 50-kHz calls induce approach behavior? PLoS One 2.

Wöhr, M., Schwarting, R.K.W., 2008. Ultrasonic calling during fear conditioning in the rat: no evidence for an audience effect. Anim. Behav. 76, 749–760.

Wöhr, M., Schwarting, R.K.W., 2009. Ultrasonic communication in rats: effects of morphine and naloxone on vocal and behavioral responses to playback of 50-kHz vocalizations. Pharmacol. Biochem. Behav. 94, 285–295.

Yusufishaq, S., Rosenkranz, J.A., 2013. Post-weaning social isolation impairs observational fear conditioning. Behav. Brain Res. 242, 142–149.

Zaki, J., Wager, T.D., Singer, T., Keysers, C., Gazzola, V., 2016. The anatomy of suffering: understanding the relationship between Nociceptive and empathic pain. Trends Cogn. Sci. 20, 249–259.

Zalaquett, C., Thiessen, D., 1991. The effects of odors from stressed mice on conspecific behavior. Physiol. Behav. 50, 221–227.

Zaniboni, C.R., Pelarin, V., Baptista-de-Souza, D., Canto-de-Souza, A., 2018. Empathy for pain: insula inactivation and systemic treatment with midazolam reverses the hyperalgesia induced by cohabitation with a pair in chronic pain condition. Front. Behav. Neurosci. 12, 1–10.

Zhou, C., Zhou, Z., Han, Y., Lei, Z., Li, L., Montardy, Q., Liu, X., Xu, F., Wang, L., 2018. Activation of parvalbumin interneurons in anterior cingulate cortex impairs observational fear. Sci. Bull. 63, 771–778.