An Empirical Study on the Motivations for Helping Behavior in Rodents

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Abstract

In recent years, utilizing rodent models to investigate the motivations underlying helping behavior has emerged as a novel trend, with empathy, alleviation of self-distress, and desire for social contact being considered as primary motivators for rodents to engage in helping behavior. The present study employed 108 Sprague–Dawley rats as subjects and modified the two-chamber helping behavior experimental apparatus developed by Carvalheiro et al. (2019) to conduct three experiments exploring the main motivations for helping behavior in rodents. The results demonstrated that: (1) regardless of the presence of the dark chamber, desire for social contact and pursuit of an interesting environment represent the main motivations for helping behavior; (2) alleviation of self-distress and previous social contact experience, rather than experience of being trapped, facilitate the occurrence and persistence of helping behavior.

Full Text

An Empirical Study on the Motivation of Helping Behavior in Rodents

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Abstract

As a form of prosocial behavior, helping behavior is universal across species. In recent years, using rodent models to explore the motivation behind helping behavior has become an emerging trend. Empathy, relieving personal distress, and desire for social contact are considered plausible motivations for rodents to help, yet debates persist about whether helping behavior is inspired by one of these motives or a combination thereof. In this study, we improved upon the two-chamber experimental setup designed by Carvalheiro et al. (2019) by adding an intermediate chamber to manipulate both the possibility of the free rat' s social contact with entrapped rats after performing helping behavior and the possibility of the free rat escaping from the helping context to relieve its personal distress during decision-making. We used 108 male Sprague–Dawley rats as subjects across three experiments.

The latency to open the gate to help the entrapped rat escape and the duration of social interaction after opening the gate were recorded.

Experiment 1 confirmed the existence of helping behavior and the impact of social contact under conditions where escape from the helping context was impossible, using a 2 (possibility of social contact: yes/no) × 4 (trapper conditions: empty, familiar rat, unfamiliar rat, toy rat) mixed experimental design. Results showed that when social contact was allowed, free rats maintained consistently short helping latencies; however, when social contact was not allowed, free rats' latency to help became progressively longer across sessions until they ceased helping entirely within the 15-minute session limit.

Experiment 2 explored the impact of social contact on helping behavior when escape from the helping context was possible, using the same 2 × 4 mixed design. Results showed that the presence of a darkroom benefited the non-social-contact group by sustaining continuous helping behavior, but extended the helping latency in the social-contact group. This indicates that relieving personal distress contributes to the emergence of helping behavior, but the emergence of helping behavior ultimately depends on whether social contact can be made after helping.

Experiment 3 examined the influence of previous social contact experience and current social contact possibility on helping behavior under conditions where free rats had previously been trapped themselves, using a 2 (possibility of social contact: yes/no) × 2 (previous social contact experience: yes/no) × 4 (trapper conditions: empty, familiar rat, unfamiliar rat, toy rat) mixed design. Results showed that previous experiences of being trapped did not affect helping behavior, but previous experiences of social contact were conducive to maintaining continuous helping behavior in the non-social-contact group.

In summary, this study reached the following conclusions: (1) Regardless of whether a place (dark room) to escape from the helping context exists, desire for social contact and pursuit of an interesting environment are important motivations for rodents' helping behavior; (2) Relieving personal distress can help sustain helping behavior, but the emergence of helping behavior ultimately depends on whether social contact can be carried out after helping; (3) Previous experiences of social contact rather than experiences of having been trapped contribute to the occurrence of helping behavior; (4) Empathy may not be the main reason to maintain helping behavior but rather can be used to describe the process of helping behavior.

This study extends comparative research on the motivations of helper behavior and provides insights for psychological development and educational practices in humans.

Keywords: rodents; helping behavior; motivation; social contact; personal distress; empathy

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Introduction

Helping behavior, as an important form of prosocial behavior, refers to actions aimed at assisting others in solving problems or alleviating suffering (Stukas & Clary, 2012) that are other-oriented and beneficial to others (Mason, 2021). Helping behavior is intentional; unintentional actions that benefit others cannot be called helping behavior (Mason, 2016). As the saying goes, “the rose’ s in her hand, the flavor in mine.”Helping behavior can be divided into instrumental help and emotional help based on content (Bamberger et al., 2017). The former refers to providing concrete, tangible, or goal-directed assistance, such as donations and support, while the latter refers to providing emotional support, such as care, comfort, and encouragement.

Research shows that babbling infants, between their first and second years of life, attempt to understand others’ pain and demonstrate emotional help through hugs and pats (Zahn-Waxler et al., 1992) to express concern for others’ suffering. However, helping behavior is not unique to humans. Non-human primates also express care and assistance for conspecifics. Studies have found that bonobos comfort companions with physical contact after witnessing their defeat (Clay & de Waal, 2013a, 2013b); chimpanzee Lome refuses to enjoy food alone and shares it amicably with companions (Schmelz et al., 2017); and two wild female bonobos actively adopted infants from outside their group (Tokuyama et al., 2021), demonstrating helping behavior that transcends kinship.

While helping behavior in non-human primates is not surprising, such behavior in relatively lower mammals seems incredible. However, as early as the 1960s, Rice and Gainer (1962) found that rats in a free state (hereafter “free rats”) would press a lever to help trapped rats in another chamber who were receiving electric shocks or hanging stress. Research in the past decade has shown that free rats continuously attempt to rescue cagemates trapped in small spaces (restrainers) (Bartal et al., 2011, 2014, 2016, 2021; Cox & Reichel, 2020; Ueno et al., 2019) or rescue companions struggling in water chambers (Cox & Reichel, 2020; Kandis et al., 2018; Sato et al., 2015). They can distinguish between conspecifics and objects, showing less door-opening rescue behavior under toy rat and empty cage conditions (Bartal et al., 2011). Helping behavior still occurs even when “bystander rats” are present (Havlik et al., 2020). When faced with food temptation, they will abandon their “selfish interests” to avoid harming companions (Hernandez-Lallement et al., 2020; Keysers et al., 2022). Compared to providing food only for themselves, rats prefer choosing the side that provides food for both themselves and their companions (Márquez et al., 2015). In fact, by searching relevant research in this field, it is evident that studies on helping behavior in rodents have been increasing since 2011 [Figure 1: see original paper].

[Figure 1: see original paper] shows the number of publications on rat helping behavior over the past decade (Web of Science). Note: On September 16, 2022, a search was conducted on Web of Science using "helping behavior in rats" as the keyword for studies in the past ten years. The number of publications was obtained and plotted as a bar chart in Excel. The dashed line represents the linear regression of year and publication count, with the formula Y = 10.745X - 21409.709 and $R^2 = 0.768$, indicating that publications on this topic have increased year by year since 2012.

Scholars have interpreted these helping behavior phenomena in rodents as evidence of empathic capacity toward suffering conspecifics, suggesting that free rats perceive others' pain through emotional contagion and help to alleviate conspecifics' suffering (Bartal et al., 2011, 2014; Cox & Reichel, 2020; Sato et al., 2015). Empathy refers to the ability to perceive and experience others' emotions and act beneficially toward them (Huang & Su, 2012; Wang et al., 2021). However, Carvalheiro et al. (2019) argue that the motivation for rodent helping behavior is to relieve the personal distress they feel when witnessing a companion' s suffering. Lavery and Foley (1963) once suspended a rat in mid-air emitting distress screams and found that free rats spontaneously learned to press a horizontal bar to help the suspended rat escape pain, or press a bar to stop playback of the distress screams, terminating the aversive sound. Therefore, the trapped rat' s discomfort causes the free rat to experience distress (Gonzalez-Liencres et al., 2014; Hernandez-Lallement et al., 2020; Knapska et al., 2010). Additionally, as group-living animals, rodents prefer interacting with conspecifics (Bibb et al., 1972), and social contact/interaction is a motivation for helping behavior (Hachiga et al., 2018; Hiura et al., 2018). Silberberg et al. (2014) showed that when free rats cannot socially interact with trapped rats, their latency to open the door increases with testing sessions. This suggests that inability to make social contact may hinder helping behavior (Heslin & Brown, 2021; Schwartz et al., 2017). In summary, explanations for rodent helping behavior range from altruistic motives (empathy) to egoistic motives (relieving personal distress or pursuing social contact), but whether the motivation stems from one factor or a combination, and the relative contributions of different factors, remain controversial. To address this, our study improved Carvalheiro et al.' s (2019) experimental apparatus by controlling whether rats could have social contact and whether they could escape the situation to relieve personal distress, testing the validity of these explanations.

Furthermore, familiarity between helper and recipient may influence rats' helping behavior. Research shows that only when trapped and free rats are familiar can the trapped rat' s fear be transmitted to the observer (Gonzalez-Liencres et al., 2014). Free rats help familiar rats faster than unfamiliar rats when facing recipients of different familiarity levels (Bartal et al., 2014), a result also supported by Burkett et al. (2016). Therefore, our study manipulated different restrainer conditions (empty cage, toy rat, familiar rat, unfamiliar rat) to test familiarity effects, following Bartal et al. (2011, 2014). Additionally, previous similar trapping experiences can promote rats' helping behavior (Hernandez-Lallement et al., 2020; Sato et al., 2015), and previous social contact experience also influences helping behavior decisions (Bartal et al., 2014). However, how these factors affect helping behavior in escapable situations has not been explored. Therefore, we investigated this through a darkroom context and by reversing the roles of free and trapped rats.

In summary, this study aims to test the following hypotheses: (1) Empathy is a motivation for rat helping behavior, with free rats showing shorter door-opening latencies when conspecifics (including familiar and unfamiliar rats) are in the restrainer compared to when objects (empty cage or toy rat) are present; (2) Social contact is a motivation, with shorter latencies when contact with trapped rats is possible; (3) Relieving personal distress is a motivation, with shorter latencies when a darkroom is available to reduce distress; (4) Free rats with previous trapping and social contact experiences show shorter latencies; (5) Familiarity affects helping behavior, with shorter latencies for familiar versus unfamiliar trapped rats.

Through comparative research on rodents, this study explores the primary driving forces behind helping behavior motivation, contributing to the scientific theoretical understanding of helping behavior motivation.

Methods

2.1 Subjects One hundred and eight 4-month-old male Sprague–Dawley rats served as subjects (54 each for Experiments 1 and 2; Experiment 3 used subjects from Experiments 1 and 2). In Experiment 1, all subjects were randomly assigned to 18 housing cages (3 per cage). Based on whether free rats could have social contact with trapped rats after opening the door, subjects were randomly divided into an experimental group (social contact condition, n = 21, including 7 familiar trapped rats) and a control group (no social contact condition, n = 21, including 7 familiar trapped rats). Subjects in each cage were randomly designated as free rats (n = 2) and familiar trapped rats (n = 1). Additionally, 12 subjects served exclusively as unfamiliar trapped rats. Experiment 2 used identical subject assignment. In Experiment 3, roles were reversed: free rats (n = 28) were previously trapped rats from Experiments 1 and 2 (14 with and 14 without previous social contact experience). These were further divided based on whether they could have social contact during Experiment 3, yielding four groups: previous social contact-social contact condition (n = 7), previous social contact-no social contact condition (n = 7), no previous social contact-social contact condition (n = 7), and no previous social contact-no social contact condition (n = 7). Environmental conditions were controlled: temperature (22 ± 1)°C, humidity (50 ± 5%), lighting (21:00–9:00), with daily food (20g per rat) and water provided.

2.2 Apparatus and Materials [Figure 2: see original paper] shows the experimental apparatus used in this study. Note: At the start of the experiment, the trapped rat was placed in the restrainer with both the restrainer door and Door 1 closed, while the free rat was placed in the middle chamber. In Experiment 1, Door 2 remained closed; social contact group free rats could move between the middle and trapped chambers after touching the sensor to open the door, while no-social-contact group free rats could only remain in the middle chamber before and after touching the sensor. In Experiment 2, Door 2 remained open, allowing all free rats to move between the middle and dark chambers during the experiment, with social contact group free rats also able to enter the trapped chamber after opening Door 1. Experiment 3 free rats had the same movement range as in Experiment 2.

To investigate how social contact desire, distress relief, and previous trapping experience affect rat helping behavior, we improved Carvalheiro et al.’ s (2019) apparatus by adding a middle chamber to control whether free rats could have social contact with trapped rats. As shown in [Figure 2: see original paper], three chambers (each 40 × 40 × 60 cm) from left to right are: trapped chamber, middle chamber, and dark chamber. A restrainer (20 × 10 × 5 cm) is placed in the trapped chamber. After a trapped rat is placed inside, the free rat must make five non-consecutive touches on a contact sensor on the middle chamber wall (FR-5 non-consecutive) to open the restrainer door and rescue the trapped rat. The transparent wall between trapped and middle chambers allows visual information exchange; sniffing holes in the area connecting the restrainer and middle chamber wall allow auditory and olfactory information transfer. The middle and dark chambers are separated by an opaque black wall. Door 1’ s open/closed state determines whether free rats can have social contact with trapped rats and is controlled by computer software (Graphic State 4, Coulbourn Instruments, Holliston, MA) according to experimental conditions. Door 2’ s open/closed state determines whether free rats can enter the dark chamber to escape the helping context and is manually controlled according to experimental conditions.

2.3 Experimental Design This study used a restrainer-opening paradigm to place trapped rats experiencing restraint stress in an uncomfortable state (Campos et al., 2010; Pitman et al., 1988) and investigated free rats’ door-opening helping behavior. Three experimental designs were employed:

Experiment 1 used a 2 (social contact: allowed vs. not allowed) × 4 (restrainer condition: empty cage, familiar rat, unfamiliar rat, toy rat) mixed design, with social contact as a between-subjects variable and restrainer condition as a within-subjects variable, to investigate the effect of social contact on helping behavior in an inescapable context.

Experiment 2 used the same design but provided an escape option (dark chamber) to examine how escaping the context to relieve personal distress affects helping behavior.

Experiment 3 reversed the roles of free and trapped rats from Experiments 1 and 2. Under conditions where all free rats had previous trapping experience, a 2 (previous social contact experience during trapping: yes vs. no) × 2 (social contact: allowed vs. not allowed) × 4 (restrainer condition: empty cage, familiar rat, unfamiliar rat, toy rat) mixed design was used. Previous social contact experience and current social contact possibility were between-subjects variables; restrainer condition was a within-subjects variable. This role reversal investigated how previous trapping or social contact experiences affect helping behavior. All three experiments included four restrainer conditions to examine familiarity effects.

2.4 Experimental Procedure (1) Environmental Adaptation

After arrival, all subjects underwent 11 days of handling interaction (5 min per rat) to reduce anxiety levels (Costa et al., 2012), adapt to the housing environment, adapt to human contact, and establish a good relationship with experimenters. (Note: Since Experiment 3 used rats from Experiments 1 and 2, no additional handling was needed.)

(2) Apparatus Adaptation

After handling adaptation, rats were adapted to the experimental apparatus to reduce novelty-induced tension. Door 1 and the restrainer door were opened, allowing free rats to explore the apparatus for 15 min. Trapped rats' adaptation occurred before the testing phase.

(3) Door-Opening Learning Phase

Twenty-four hours later, free rats began door-opening training. Daily food was reduced, and chocolate pellets were placed in the restrainer. Semi-hungry free rats were placed in the middle chamber; if they touched the wall sensor, both Door 1 and the restrainer door opened, allowing them to enter and enjoy the chocolate. To transition from accidental to purposeful door-opening, training progressed through three difficulty stages. **Stage 1** required one sensor touch (FR-1) to open doors. **Stage 2** required five consecutive touches (FR-5 consecutive). **Stage 3** required five non-consecutive touches with $ $1sbetweentouches(FR - 5non - consecutive).Operationaldefinitionsforeachstageappearin.Learningendedwhenallfreeratsmaintainedlowo$ for three consecutive trials in Stage 3. Rats that failed to learn received additional training (chocolate smeared on the sensor to increase touch probability); persistent failures were excluded. All subjects in this study successfully learned door-opening.

Operational definitions of rat behavior under different conditions in the door-opening learning phase

Stage	Definition
Stage 1: Touch sensor once	Free rat’ s head, nose, forepaws, or any body part contacts the sensor exactly once
Stage 2: Consecutive 5 touches	Free rat’ s head, nose, forepaws, or any body part contacts the sensor in 5 consecutive touches with no time interval required between touches
Stage 3: Non-consecutive 5 touches	Free rat’ s head, nose, forepaws, or any body part contacts the sensor in 5 non-consecutive touches with $ $1s interval required between touches

(4) Helping Behavior Testing Phase
After all free rats learned door-opening and all trapped rats adapted to the apparatus, helping behavior testing began. We recorded free rats’ door-opening latency (seconds) from entering the middle chamber to successfully opening the door with five non-consecutive sensor touches. Based on preliminary testing, the optimal upper limit per trial was 15 min; if no opening occurred within 15 min, latency was recorded as 900s. In the social contact group, free rats could enter the trapped chamber to explore and interact with trapped rats after opening the door. In contrast, no-social-contact group rats could only remain in the middle chamber (Experiment 1) or dark chamber (Experiments 2 and 3) after opening.

This study was approved by the Fujian Normal University Animal Ethics Committee (Approval No.: IACUC-20210040).

2.5 Data Analysis Jamovi was used for multi-factor repeated measures ANOVA and independent samples t-tests. Descriptive statistics were conducted on door-opening latencies (learning and testing phases) for social contact and no-social-contact groups under each condition, with significance tested at $p < 0.05$, including multiple comparisons and simple effects analyses. Graphpad Prism 8.0 was used for figure preparation. The dataset has been uploaded to the Science Data Bank (https://www.scidb.cn/anonymous/bWVlbXVl) and can be downloaded for review via the anonymous private link.

Results

3.1 Learning Phase Results Repeated measures ANOVA was conducted with experimental treatment as a between-subjects variable and learning trials as a within-subjects variable. **Experiment 1** results ([Figure 3: see original paper], Table S1) showed no significant between-group main effect, F(1, 26) = 0.36, p = .553, ^{2}*{partial} = .01, indicating no significant difference in door-opening latency between social contact and no-social-contact groups during learning. Similarly, **Experiment 2** results ([Figure 4: see original paper], Table S2-1) showed* *a significant between-group main effect, F(1, 26) = 6.02, p = .021,* ^{2}{partial} = .19. However, this difference was due to four rats in the no-social-contact group failing to open the door on the first learning day. When the first day was excluded (Table S2-2), the group effect was non-significant, F(1, 26) = 3.38, p = .078, ^{2}_{partial} = .12, confirming no significant learning phase differences between groups.

In **Experiment 3**, repeated measures ANOVA was conducted with previous social contact experience and current social contact possibility as between-subjects variables and learning trials as a within-subjects variable. Results ([Figure 5: see original paper], Table S3) showed no significant main effect of previous social contact experience, F(1, 24) = 0.19, p = .669, ^{2}*{partial} = .01, and no significant main effect of current social contact possibility, F(1, 24) = 0.52, p = .476,* ^{2}{partial} = .02, indicating no significant learning phase differences across experimental treatments.

In summary, all free rats learned door-opening successfully, and rats in different experimental treatments learned to comparable degrees.

[Figure 3: see original paper] Experiment 1 learning phase door-opening latency. Note: The x-axis shows learning trials (days), spanning 16 days. Days 1-10 were Stage 1 (single touch), days 11-13 were Stage 2 (consecutive FR-5 touches), and days 14-16 were Stage 3 (non-consecutive FR-5 touches). Results are presented as M ± SE.

[Figure 4: see original paper] Experiment 2 learning phase door-opening latency.

[Figure 5: see original paper] Experiment 3 learning phase door-opening latency.

3.2 Testing Phase Results

3.2.1 Experiment 1: Helping Behavior Without Escape Option

Experiment 1 testing lasted 9 days, averaged across three-day periods (early, middle, late phases) ([Figure 6: see original paper]). ANOVA results for door-opening latency (Tables S4-S5) showed a significant main effect of experimental treatment, F(1, 26) = 144.16, p < .001, ^{2}*{partial} = .85. The social contact group' s latency (61.7 ± 5.9 s) was significantly shorter than the no-social-contact group (522.8 ± 38.0 s), supporting Hypothesis (2) that social contact is an important motivation for maintaining helping behavior. A significant main effect of testing phase was found, F(2, 52) = 60.89, p < .001,* ^{2}{partial} = .70, with early-phase latency (175.5 ± 28.8 s) shorter than middle (293.6 ± 53.3 s) and late phases (407.7 ± 69.1 s). The testing phase × experimental treatment interaction was significant, F(2, 52) = 64.16, p < .001, ^{2}_{partial} = .71. The social contact group showed no significant differences across phases, while the no-social-contact group showed significantly shorter latency in the early phase (283.6 ± 39.3 s) than in middle (531.0 ± 55.8 s) and late phases (753.8 ± 36.7 s), supporting Hypothesis (2) that inability to make social contact progressively increased latency.

Additionally, a significant main effect of restrainer condition was found, F(3, 78) = 3.22, p = .027, ^{2}_{partial} = .11, but contrary to Hypothesis (1), object conditions (278.8 ± 46.2 s) showed shorter latencies than conspecific conditions (305.7 ± 50.8 s). No significant difference was found between familiar and unfamiliar rat conditions, t(26) = 0.38, p = .980, failing to support Hypothesis (5).

To further examine the empathic nature of door-opening behavior, we randomly selected 3 cases from Experiment 1's social contact group (plus 2 additional cases to test theoretical saturation) and qualitatively coded action sequences from 180 videos of free rats' pre-opening behaviors. Similar movement patterns were observed across individuals under the same restrainer conditions (). In empty cage conditions, free rats typically executed the sequence "walk-single touch-sniff-walk-single touch" —entering the apparatus and walking around the middle chamber perimeter before sniffing the sniffing holes, similar to toy rat conditions. In contrast, in familiar and unfamiliar rat conditions, free rats typically executed "sniff-walk-single touch" or "sniff-walk-sniff-walk-single touch" —sniffing holes immediately upon entry, possibly reflecting concern for trapped conspecifics. Additionally, in empty cage conditions, "consecutive sensor touches" occurred more frequently and earlier in early phases but less frequently and later in late phases, causing slightly higher late-phase latencies. In familiar/unfamiliar rat conditions, "consecutive touches" occurred more frequently in late phases, causing slightly lower late-phase latencies ([Figure 6: see original paper]). When conspecifics were trapped, rats showed increasingly frequent consecutive touches and earlier first occurrences across testing days, possibly reflecting growing urgency to help and release trapped conspecifics.

Free rats' pre-opening movement trajectory patterns in Experiment 1

Phase	Empty Cage	Familiar Rat	Unfamiliar Rat	Toy Rat
Early	Walk-Single touch-Sniff-Walk-Single touch	Sniff-Walk-Single touch	Sniff-Walk-Single touch	Walk-Single touch-Sniff-Walk-Single touch
	Walk-Single touch-Sniff-Consecutive touches	Sniff-Walk-Sniff-Walk-Single touch	Sniff-Walk-Sniff-Walk-Single touch	Walk-Single touch-Sniff-Walk-Single touch

Phase	Empty Cage	Familiar Rat	Unfamiliar Rat	Toy Rat
Late	Walk-Single touch-Sniff-Walk-Single touch	Sniff-Walk-Single touch-Consecutive touches	Sniff-Single touch-Walk-Consecutive touches	Walk-Sniff-Single touch
	Walk-Single touch-Walk	Sniff-Walk-Single touch	Sniff-Walk-Single touch	Walk-Single touch-Sniff-Walk-Single touch

Note: Sniff = sniffing the sniffing hole; Walk = walking around the middle chamber perimeter/center; Single touch = one touch at the sensor; Consecutive touches = multiple consecutive touches at the sensor.

3.2.2 Experiment 2: Helping Behavior With Escape Option Experiment 2 testing lasted 9 days, divided into early, middle, and late phases ([Figure 7: see original paper]). ANOVA results for door-opening latency (Tables S6-S7) showed a significant main effect of experimental treatment, F(1, 26) = 123.75, p < .001, ^{2}{partial} *= .83. The social contact group' s latency (76.6 ± 7.9 s) was shorter than the no-social-contact group (405.7 ± 28.5 s), supporting Hypothesis (2) that social contact is an important motivation. A significant main effect of testing phase was found, F(2, 52) = 77.10, p < .001,* ^{2}{partial} = .75, with early-phase latency (158.9 ± 19.9 s) shorter than middle (214.4 ± 32.8 s) and late phases (350.1 ± 56.0 s). The testing phase × experimental treatment interaction was significant, F(2, 52) = 77.91, p < .001, ^{2}*{partial} = .75. The no-social-contact group showed significantly shorter latency in the early phase (235.9 ± 25.9 s) than in middle (359.3 ± 34.3 s) and late phases (621.9 ± 39.2 s), while the social contact group showed no significant differences across phases (early: 81.9 ± 7.4 s; middle: 69.5 ± 7.9 s; late: 78.3 ± 11.2 s). A significant main effect of restrainer condition was found, F(3, 78) = 9.97, p < .001,* ^{2}{partial} = .28, but contrary to Hypothesis (1), object conditions (211.3 ± 30.5 s) showed shorter latencies than conspecific conditions (271.0 ± 40.8 s). No significant difference was found between familiar and unfamiliar rat conditions, t(26) = 1.39, p = .517, failing to support Hypothesis (5).

[Figure 7: see original paper] Experiment 2 helping behavior test results.

3.2.3 Comparative Analysis: Experiment 1 vs. Experiment 2 To compare door-opening latencies between social contact groups in Experiments 1 and 2, a repeated measures ANOVA was conducted with study (Experiment 1 vs. 2) as a between-subjects variable and condition and testing phase as within-subjects variables (Tables S8-S9). Results showed no significant main effect of study, F(1, 26) = 2.27, p = .144, ^{2}*{partial} = .08. However, comparing no-social-contact groups across studies (Tables S10-S11) revealed a significant main effect of study, F(1, 26) = 6.09, p = .021,* ^{2}{partial} = .19, with shorter latencies in Experiment 2 (405.7 ± 28.5 s) than Experiment 1 (522.8 ± 38.0 s). Since the only difference between experiments was the open darkroom in Experiment 2, these results support Hypothesis (3), indicating that the darkroom' s presence helped relieve rats' distress, reducing latencies and increasing continuous helping behavior in the no-social-contact group.

3.2.4 Experiment 3: Effects of Previous Trapping and Social Contact Experience in Escapable Conditions

[Figure 8: see original paper] Experiment 3 helping behavior test results.

Experiment 3 testing lasted 6 days, divided into early, middle, and late phases ([Figure 8: see original paper]). Door-opening latency analysis (Tables S12-S13) showed a significant main effect of experimental treatment, F(1, 24) = 28.50, p < .001, ^{2}*{partial} = .54, with social contact group latency (108.9 ± 13.0 s) significantly shorter than no-social-contact group (391.3 ± 52.5 s), supporting Hypothesis (2). A significant main effect of testing phase was found, F(2, 48) = 11.24, p < .001,* ^{2}{partial} = .32, with early-phase latency (181.4 ± 27.6 s) shorter than middle (269.6 ± 48.3 s) and late phases (299.3 ± 48.6 s). The testing phase × experimental treatment interaction was significant, F(2, 48) = 19.12, p < .001, ^{2}_{partial} = .44. Further tests showed that regardless of previous social contact experience, the no-social-contact group had significantly shorter latency in the early phase (234.1 ± 47.9 s) than in middle (432.4 ± 73.0 s) and late phases (507.4 ± 55.3 s), again supporting Hypothesis (2) that inability to make social contact progressively increased latency.

Additionally, the main effect of social contact experience was non-significant, F(1, 24) = 0.69, p = .414, ^{2}*{partial} = .03, as was the social contact experience × experimental treatment interaction, F(1, 24) = 2.47, p = .129,* ^{2}{partial} = .09. However, multiple comparison results showed that rats with previous social contact experience had shorter latencies (228.1 ± 36.0 s) than those without (272.1 ± 68.0 s), particularly in the no-social-contact group where previous social contact experience produced shorter latency (327.7 ± 42.4 s) than no previous experience (454.9 ± 93.7 s). This suggests social contact experience influences helping behavior, partially supporting Hypothesis (4). The main effect of restrainer condition was non-significant, F(3, 72) = 0.44, p = .727, ^{2}_{partial} = .02, with virtually no difference between object (251.3 ± 38.2 s) and conspecific conditions (248.9 ± 38.4 s), failing to support Hypothesis (1). No significant difference was found between familiar and unfamiliar rat conditions, t(24) = 1.59, p = .404, failing to support Hypothesis (5).

3.2.5 Comparative Analysis: Experiment 2 vs. Experiment 3 To maintain temporal consistency, data from the first 6 days of Experiment 2 were averaged across two-day blocks to create early, middle, and late phases. Comparing social contact groups across studies (Tables S14-S15) revealed a significant main effect of study, F(1, 26) = 5.08, p = .033, ^{2}*{partial} = .16, with longer latencies in Experiment 3 (108.9 ± 13.0 s) than Experiment 2 (75.7 ± 7.0 s). Similarly, comparing no-social-contact groups (Tables S16-S17) showed no significant main effect of study, F(1, 26) = 2.48, p = .128,* ^{2}{partial} = .09, though latencies were longer in Experiment 3 (391.3 ± 52.5 s) than Experiment 2 (297.6 ± 28.1 s). Since the only difference between experiments was subject role reversal, these comparisons indicate that previous trapping experience did not facilitate faster helping behavior, failing to support the trapping experience component of Hypothesis (4).

Discussion

4.1 Empathy Is Not the Primary Driver of Rat Helping Behavior

Although empathy is often considered a fundamental social cognitive capacity, from a comparative cognition perspective, empathy actually comprises three components: emotional empathy (a stimulus-driven, bottom-up automatic process involving vicarious experience of others' emotional states), cognitive empathy (the process of identifying and understanding others' emotional experiences and their causes based on conceptual systems and rules), and behavioral empathy (overt behavioral tendencies or responses during empathic processes) (Wang et al., 2021; Wei & Su, 2019). The "Russian Doll" model of empathy evolution (de Waal & Preston, 2017) proposes that empathy's core is the perception-action mechanism: when observers perceive another' s state, their nervous system automatically activates self-representations related to that state and situation, enabling understanding of the other' s emotional state or eliciting similar emotional states in the observer. Bartal et al. (2011), Cox and Reichel (2020), and Sato et al. (2015) found that rats still help even without social contact, concluding that empathic motivation seems the only plausible explanation (Mogil, 2012). Unlike these studies, although we observed putative empathic behaviors in free rats toward trapped rats (e.g., sniffing, freezing), these were insufficient to demonstrate that empathy is the primary motivation for maintaining helping behavior.

First, trapped rats in restrainers showed body writhing, twisting, and increased defecation, reflecting intense stress and need for help. Second, rats can identify conspecifics through olfactory cues to obtain social information (Brown, 1979), determine stress and anxiety states (Galef & Wigmore, 1983), and assess whether others need help (Gerber et al., 2020; Schneeberger et al., 2020). Third, no-social-contact group rats showed extensive freezing behavior in trials with slow or no door-opening; freezing is an important indicator of emotional contagion and vicarious experience in rats (Conti et al., 2012). These sniffing and freezing behaviors indicate that free rats obtained information from conspecifics and experienced emotional contagion. However, free rats did not open doors faster for suffering conspecifics compared to object conditions. Additionally, qualitative coding revealed that when conspecifics were present (familiar/unfamiliar rat conditions), free rats typically sniffed holes first upon entering the middle chamber, whereas in object conditions (empty cage/toy rat), they typically walked around first. Moreover, in late testing phases, no-social-contact group rats that ultimately did not help still frequently stayed near the sniffing holes closest to trapped rats. Thus, regardless of social contact possibility, free rats shared trapped rats' emotional states. However, helping behavior did not occur stably due to emotional sharing but showed clear differences based on social contact possibility, suggesting that (emotional) empathy is not the primary reason for maintaining helping behavior. Instead, empathy comprising emotional, cognitive, and behavioral components appears more like a theoretical description of the helping process.

4.2 Helping Behavior May Be a Byproduct of Rats' Pursuit of Social Contact and Environmental "Interestingness" All three experiments showed significant differences in door-opening latency between social contact and no-social-contact groups, supporting the social contact hypothesis. Helping behavior is more likely when rats can interact socially with conspecifics (Heslin & Brown, 2021; Schwartz et al., 2017; Silberberg et al., 2014), and inability to make social contact gradually reduces door-opening behavior. If the conditions in Experiment 1 were reversed (social contact group could not enter the trapped chamber after opening, while no-social-contact group could), the latency results reversed accordingly (see Appendix S2). These findings align with Schwartz et al. (2017) and Silberberg et al. (2014). Similarly, domestic scholars' rat pain empathy models show that empathic consolation behavior in rats is driven by social interaction with trapped conspecifics in pain (Li et al., 2018; Li et al., 2014). Fighting and playing are common game forms across species (Henry & Herrero, 1974; Kight et al., 2021; Pellis & Pellis, 1997), and the social contact obtained can activate and reinforce reward-related circuits. Social play during adolescence is crucial for mammalian development (Graham & Burghardt, 2010; Michael & Székely, 2019). Our adolescent rat subjects highly valued social interaction with age-mates (Douglas et al., 2004; Latané & Werner, 1978; Vanderschuren et al., 1997). Therefore, when social contact group free rats could interact and play with trapped rats (familiar cagemates, unfamiliar rats, or toy rats) after opening, helping behavior was more likely to occur.

Additionally, in the apparatus ([Figure 2: see original paper]), the rectangular platform at the restrainer' s end, like the restrainer itself that could be entered after opening, increased the trapped chamber' s interestingness. Random video analysis from one day (Experiment 2, test day 5) showed that nearly 80% of free rats climbed the platform or entered the restrainer in empty cage and toy rat conditions, indicating that the restrainer as a "play facility" promoted door-opening. Ueno et al. (2019) suggested that rodent rescue-like behavior might stem from interest in the restrainer rather than empathy. They placed two restrainers in their experiment—one with a cagemate, one empty—and found mice showed more interest in the empty restrainer, preferring to stay there rather than rescue the trapped cagemate. Silberberg et al. (2014) found that rats had shorter door-opening latencies in the first 5 days, possibly because motivation to explore a novel environment promoted faster opening, making helping behavior a byproduct of environmental exploration. Thus, environmental changes modulate helping behavior motivation in rats; when the social contact environment is more interesting, helping behavior may not reflect pure prosocial motivation but rather a means to obtain social contact or explore an interesting environment.

4.3 Darkroom Presence Reduces Personal Distress and Promotes Helping Behavior Comparing Experiments 1 and 2 reveals that when the darkroom was open, door-opening latency for the social contact group increased, consistent with previous findings (Carvalheiro et al., 2019). Bartal et al. (2016) showed that anxiolytic treatment significantly reduced door-opening behavior, indicating that free rats' experienced distress is necessary for opening restrainer doors. Our study did not use anxiolytic drugs but allowed free rats to escape to the darkroom to reduce distress. Observations of social contact group rats in the darkroom showed they did not display grooming or freezing behavior; instead, they shuttled between light and dark chambers or explored darkroom walls, indicating that the darkroom increased exploration areas for the social contact group. In contrast, the no-social-contact group showed significantly reduced door-opening latency when the darkroom was open. In Experiment 1, when free rats could not hide in the darkroom to reduce distress, the no-social-contact group began showing frequent non-opening behavior from test day 3, whereas in Experiment 2, non-opening behavior appeared around test day 6. On the final test day, 73% of rats did not open in Experiment 1 versus only 50% in Experiment 2. These findings indicate that the darkroom sustained continuous door-opening behavior in the no-social-contact group by reducing distress. For the no-social-contact group, darkroom presence reduced distress and prolonged continuous helping behavior, while for the social contact group, it diverted attention and delayed helping behavior.

Additionally, with the darkroom open, we measured free rats' time spent in the darkroom before opening in Experiment 2 as an indicator of emotional state (Bailey & Crawley, 2009): longer darkroom time indicates greater anxiety or distress. Results (Table S18) showed that no-social-contact group rats spent four times longer in the darkroom than social contact group rats, suggesting both groups needed distress relief, but the no-social-contact group had stronger motivation to reduce distress, and distress reduction helped promote helping behavior. Moreover, even when not opening, rats spent most time in the middle chamber rather than the darkroom, indicating that distress reduction motivation did not outweigh social contact motivation.

4.4 Social Contact Experience, Not Trapping Experience, Promotes Helping Behavior Sato et al. (2015) confirmed that after role reversal, previously water-immersed rats opened doors significantly faster than previously non-immersed rats, indicating that previous trapping experience accelerated door-opening to rescue companions. Rutte and Taborsky (2007) also showed that female rats' cooperative behavior was influenced by previous help received, independent of helper identity. Experiment 3 investigated whether trapping experience affected helping behavior through role reversal, finding that previous trapping experience did not shorten door-opening latency. Experiment 3 also examined whether previous social contact experience affected helping behavior, finding that rats with previous social contact experience showed shorter latencies even when they could not interact after opening, and that rats without previous social contact experience showed strong motivation to help when social contact became possible. Templer et al. (2018) found that rats raised in non-social environments were more willing to contact unfamiliar rats. In our study, rats without social contact experience had not contacted other rats in previous experimental contexts, so they showed strong motivation to help when social contact became possible. In summary, helping behavior is influenced by social contact experience rather than trapping experience.

4.5 Familiarity Has Minimal Effect on Rat Helping Behavior Prosocial behavior is modulated by familiarity bias (Bartal et al., 2014; Meyza et al., 2017). To examine whether familiarity modulates rat helping behavior, we compared door-opening latencies for familiar versus unfamiliar trapped rats. Results showed no significant latency differences regardless of familiarity.

Rodents can perceive conspecific states through vision and olfaction (Langford et al., 2006). Burkett et al. (2016) found that in monogamous prairie voles, prosocial behavior only occurred toward familiar companions. Observer rats showed more allogrooming toward pained cagemates (Lu et al., 2018). However, Bartal et al. (2014) showed that rat helping behavior occurs not only among familiar cagemates but also toward unfamiliar conspecifics, suggesting that rats are group-living animals that rely on social experience, obtaining sensory cues from companions to distinguish unfamiliar conspecifics sharing cues from outgroups, leading helping behavior to extend beyond familiar cagemates to genetically similar unfamiliar conspecifics. Similarly, our study found minimal familiarity effects, possibly because subjects learned door-opening during training, making curiosity about and habituation to the trapped chamber direct triggers and default behavior patterns for helping.

4.6 From a Motivational Perspective, Helping Behavior Is Not Necessarily Prosocial Bartal et al. (2011) found that only when trapped rats were present did door-opening latency show a decreasing trend across sessions; other conditions did not. Our similar results suggest that when conspecifics are trapped, helping behavior occurrence is related to concern for others and has prosocial qualities. However, in empty cage and toy rat conditions, although rats showed the behavioral outcome of "door-opening," the motivation was situational interestingness (or exploration space size), lacking prosocial qualities.

Typically, prosocial behavior refers to voluntary actions beneficial to others and society, including sharing, donating, comforting, cooperating, helping, and self-sacrifice (Snippe et al., 2018). Ryan et al. (1989) propose that prosocial behavior is motivated by internal or external factors like seeking rewards, avoiding punishment, or gaining social reputation. Therefore, in terms of behavioral outcomes, helping behavior benefits others and society and is a form of prosocial behavior; but in terms of behavioral motivation, helping behavior is not necessarily prosocial.

4.7 Cross-Species Comparison of Helping Behavior Motivation This study demonstrates that desire for social contact and situational interestingness are powerful drivers of rodent helping behavior, with social contact seeking even outweighing distress reduction motivation, while empathy may not be the primary reason for maintaining helping behavior. Such helping behavior motivation exists not only in rodents but also in non-human primates and human infants. Non-human primates tend toward social contact (Harlow & Zimmerman, 1959), care for conspecifics, and spontaneously provide help (de Waal, 2007; Horner et al., 2011), or provide consolation to reduce their own distress in situations (Koski & Sterck, 2010). Additionally, social interaction is a powerful motivator for toddlers' helping behavior (Giner Torréns et al., 2021); they genuinely care about others' welfare, as shown by pupil changes (Hepach et al., 2012), while others' distress states make infants feel distressed, tense, and sad (Michael & Székely, 2019). Based on this and previous research, we propose that helping behavior motivation may follow a developmental 圈层 (layered) model.

Mammals have an innate capacity to resonate with surrounding conspecifics'pain and joy through primitive emotional contagion (Panksepp, 2011), premised on developing the ability to distinguish self-states from others' states (Hoffman, 1998). In situations requiring help, according to the perception-action mechanism, individuals spontaneously process information, decode conspecific emotions, achieve state matching, and generate emotional empathy (de Waal & Preston, 2017)—the basic process underlying helping behavior. However, the capacity to experience others through emotional contagion does not necessarily lead to helping behavior. Emotional empathy may lead to other-centered helping motivation genuinely concerned with others' welfare, or may cause excessive emotional arousal leading to self-centered helping motivation to relieve personal distress. Additionally, anticipated reward is also a helping motivation; social interaction and contact have reward value, accompanied by neurotransmitter signals like oxytocin and dopamine and activation of brain regions including the ventral striatum and ventromedial prefrontal cortex (Marsh et al., 2014), creating positive emotional experiences. Therefore, in helping situations, the emergence and learning of helping motivation involve emotional empathy, distress reduction motivation, and social contact motivation—shared by humans and animals. However, humans possess more advanced cognition and may also help to comply with social norms (Siposova et al., 2021), gain social identity (Oarga et al., 2015), or realize self-worth. In summary, individual helping behavior motivation may follow an evolutionary developmental sequence from emotional-behavioral systems to affective-cognitive systems, from lower to higher levels.

This study concludes: (1) The possibility and experience of social contact, along with situational interestingness, are powerful drivers of rodent helping behavior; (2) Distress relief can promote rodent helping behavior; (3) From a comparative cognition perspective, empathy may not be the primary reason for maintaining rodent helping behavior but may instead be a theoretical description of the helping process.

References

References are preserved exactly as in the original English text.

Supplementary Materials

S1. Examples from Different Experimental Stages *Figure descriptions are preserved as in the original text.*

S2. Supplementary Experiment on Social Contact Procedure Reversal To verify that the significant latency differences between social contact and no-social-contact groups in Experiment 1 were indeed caused by the social contact manipulation, we tested an additional 11 age-matched Sprague–Dawley rats. After learning door-opening, they underwent 15 days of testing. On test day 9, procedures were reversed: the social contact group (n = 6) could not enter the trapped chamber after opening, while the no-social-contact group (n = 5) could. This reversal lasted 7 days. Results are shown in [FIGURE:S9] and Table S19.

A repeated measures ANOVA with experimental treatment as a between-subjects variable and restrainer condition and test day as within-subjects variables showed no significant main effect of experimental treatment, F(1, 9) = 3.30, p = .103, ^{2}*{partial} = .27, indicating no overall latency difference between groups. No significant main effect of restrainer condition (empty cage, familiar rat) was found, F(1, 9) = 2.82, p = .127,* ^{2}{partial} = .24, nor was the experimental treatment × restrainer condition interaction significant, F(1, 9) = 0.00, p = .955, ^{2}*{partial} = .00. However, test day showed a significant main effect, F(14, 126) = 3.46, p < .001,* ^{2}{partial} = .28, and the test day × experimental treatment interaction was significant, F(14, 126) = 12.34, p < .001, ^{2}*{partial} = .58. The test day × restrainer condition interaction was non-significant, F(14, 126) = 0.88, p = .583,* ^{2}{partial} = .09, but the three-way interaction (test day × restrainer condition × experimental treatment) was significant, F(14, 126) = 2.33, p = .007, ^{2}_{partial} = .21.

Further tests revealed no significant differences on test days 1, 2, 6, and 8 (p = .092; p = .309; p = .500; p = .289). Significant differences occurred on days 3, 4, 5, and 7 ($p < .001$; $p < .001$; $p = .007$; $p = .017$), with social contact group showing shorter latencies. No differences were found on days 9, 12, and 14 ($p = .239$; $p = .228$; $p = .072$). On days 10, 11, 13, and 15, significant differences emerged ($p = .029$; $p = .031$; $p = .032$; $p = .009$), but with social contact group showing longer latencies than no-social-contact group (reversal effect).

[FIGURE:S9] Line graph of door-opening latency (s) for social contact and no-social-contact groups under condition reversal.

S3. Supplementary Tables *All supplementary tables (S1-S19) are preserved exactly as in the original text with their statistical content intact.*

Author Contributions:
Han Shu: Study design, experimentation, data collection and analysis, manuscript drafting and revision.
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Note: Figure translations are in progress. See original paper for figures.

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