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Empathy and Pro-Social Behavior in Rats

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As with any method, there are limitations to the use of nighttime satellite imagery; the exact association between brightness and population density varies between locations and is affected by environmental (*15*) and economic factors (*25*–*27*). Additionally, images must be selected carefully to avoid contamination from solar and lunar illumination and cloud cover (SOM part 1).

Measuring the drivers of seasonal variability in transmission rates, particularly in areas with sparse disease surveillance and strong epidemic nonlinearities (*2*), is critical for improving the design of epidemiological control measures. It is now possible to improve outbreak response strategies based on fluctuations in population density and disease transmission, as we have shown for a recent measles outbreak in Niamey. This would be particularly useful in areas with repetitive seasonal fluctuations in density where targeted campaigns could maximize the number of individuals present during vaccinations. It is also possible that this method could be adapted for near–real-time analyses, as images are uploaded from the satellite within ~48 hours (although the usability of individual images is sensitive to environmental conditions).

The advantages of understanding changes in population density are broadly applicable. This information can aid in estimating population changes caused by large-scale human movements—i.e., displacement due to conflict (*17*) or recurring movements such as the Hajj. Measurements of fluctuations in population density provide important information to guide decisions on disease control strategies, international aid and humanitarian responses, and assessments of economic development.

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Supporting Online Material

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Empathy and Pro-Social Behavior in Rats

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Whereas human pro-social behavior is often driven by empathic concern for another, it is unclear whether nonprimate mammals experience a similar motivational state. To test for empathically motivated pro-social behavior in rodents, we placed a free rat in an arena with a cagemate trapped in a restrainer. After several sessions, the free rat learned to intentionally and quickly open the restrainer and free the cagemate. Rats did not open empty or object-containing restrainers. They freed cagemates even when social contact was prevented. When liberating a cagemate was pitted against chocolate contained within a second restrainer, rats opened both restrainers and typically shared the chocolate. Thus, rats behave pro-socially in response to a conspecific's distress, providing strong evidence for biological roots of empathically motivated helping behavior.

Pro-social behavior refers to actions that are intended to benefit another. One common motivator of pro-social behavior in humans is empathic concern: an other-oriented emotional response elicited by and congruent with the perceived welfare of an individual in distress (*1*, *2*). Sharing another's distress via emotional contagion can result in overwhelming fear and immobility unless one's own distress is down-regulated, thus allowing empathically driven pro-social behavior (*3*, *4*). Building on observations of emotional contagion in rodents (*5*–*10*), we sought to determine whether rats are capable of empathically motivated helping behavior. We tested whether the presence of a trapped cagemate induces a pro-social motivational state in rats, leading them to open the restrainer door and liberate the cagemate.

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Rats were housed in pairs for 2 weeks before the start of testing. In each session, a rat (the free rat) was placed in an arena with a centrally located restrainer in which a cagemate was trapped (trapped condition, $n = 30$ rats, 6 females). The free rat could liberate the trapped rat by applying enough force to tip over the restrainer door (Fig. 1A). If a free rat failed to open the door, the experimenter opened it halfway, allowing the trapped rat to escape and preventing learned helplessness. Rats remained in the arena together for the final third of the session. Door-opening only counted as such if the free rat opened the door before the experimenter opened it halfway. Sessions were repeated for 12 days. Control conditions included testing a free rat with an empty restrainer (empty condition, $n = 20$ rats, 6 females) or toy rat–containing restrainer (object condition, $n = 8$ males). As an additional control, for the number of rats present, we tested a free rat with an empty restrainer and an unrestrained cagemate located across a perforated divide (2+empty condition, $n = 12$ males). Free rats' heads were marked and their movements were recorded with a top-mounted camera for offline analysis (*11*).

Free rats circled the restrainer, digging at it and biting it, and contacted the trapped rat through holes in the restrainer (Fig. 1B and movie S1). They learned to open the door and liberate the trapped cagemate within a mean of 6.9 ± 2.9 days. Free rats spent more time near the restrainer in

the arena center [$P < 0.001$, mixed model analysis (MMA), Fig. 1C] and showed greater movement speed (hereafter termed activity, $P < 0.001$, MMA, Fig. 1D) than did control rats. Before learning to open the restrainer door, free rats in the trapped condition stayed significantly more active in the second half of sessions relative to the first half than did rats in control conditions [$P < 0.001$, MMA, protected least significant difference (PLSD) test, Fig. 1E]. Thus, rats were motivated to move and act specifically in the presence of a trapped cagemate.

In the trapped condition, the proportion of rats that opened the door increased (Fig. 2A), and the latency to door-opening decreased (Fig. 2B and movie S2) across sessions, which is evidence of learning. Significantly more rats in the trapped [23 out of 30 (23/30)] than control (5/40) conditions were classified as "openers" by the end of the experiment ($P < 0.001$, χ-square test), opening the door within minutes of placement in the arena (*11*). A sharp increase in the free rat's activity was observed at the time of door-opening (Fig. 2C), suggesting that the liberation of a trapped cagemate is a salient event.

Initially, rats in the trapped condition opened the door in any of three ways: tipping the door over from the side or top or pushing it up with their heads. However, on days 6 to 12, they consistently opened the door with their heads (Fig. 2D). Furthermore, whereas rats initially froze after the door fell over, later on they did not freeze (Fig. 2E), demonstrating that door-opening was the expected outcome of a deliberate, goal-directed action.

Ultrasonic (~23 kHz) vocalizations were collected from multiple testing arenas with a bat-detector and were analyzed to determine whether rats emitted alarm calls. Significantly more alarm calls were recorded during the trapped condition (13%) than during the empty and object conditions [3 to 5%, $P < 0.05$ analysis of variance (ANOVA), PLSD < 0.05, Fig. 2F] in randomly sampled files from all days of testing. Alarm calls occurred more frequently (20 to 27%) on days 1 to 3, when door-opening was rare. In 90% of files containing alarm calls on day 1, the trapped rat was identified as the source; in the remaining samples, we were not able to identify the caller. These data suggest that trapped rats were indeed stressed.

A greater proportion of female rats (6/6) than male rats (17/24) in the trapped condition became door-openers ($P < 0.05$, χ-square), which is consistent with suggestions that females are more empathic than males (*7*, *12*, *13*). Further, female rats in the trapped condition opened the restrainer door at a shorter latency than males on days 7 to 12 ($P < 0.01$, MMA, Fig. 3A). Female rats were also more active than males in the trapped condition ($P < 0.001$, ANOVA) but not in the empty condition (Fig. 3B).

To examine whether individual differences in boldness influenced door-opening, we tested the latency for approach to the ledge of a half-opened

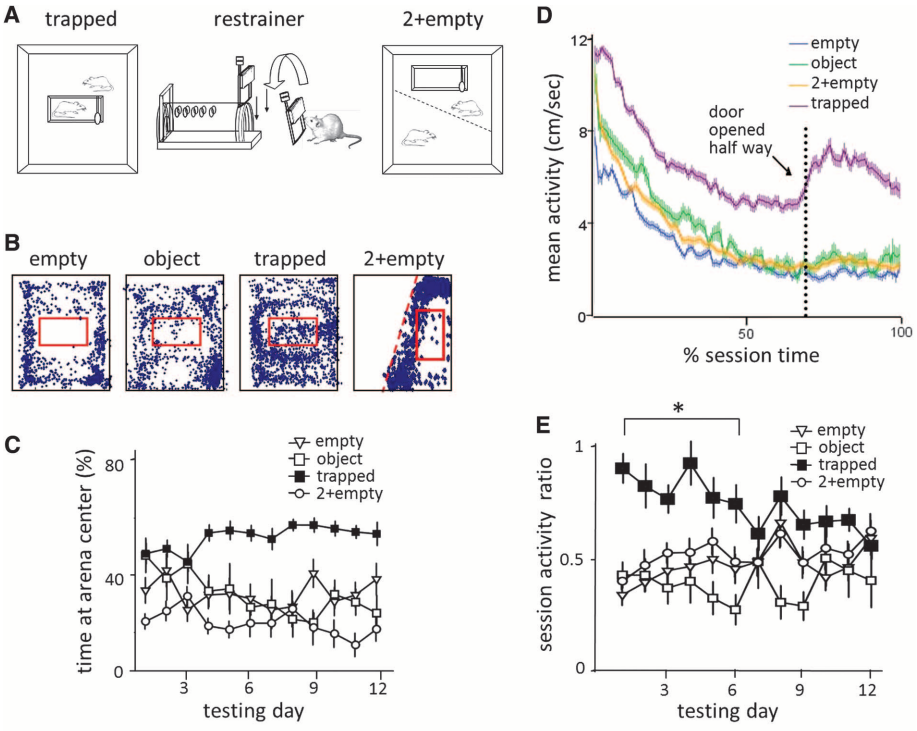

Fig. 1. (**A**) Top views of the trapped and 2+empty conditions and side views of the restrainer and door. (**B**) The locations (0.5 frames per second) of representative free rats with respect to the restrainer (red box) are plotted for each condition on day 1 of testing. (**C**) Rats in the trapped condition spent more time (mean ± SEM) in the arena center (>5 cm away from the wall) than did rats in control conditions. (**D**) The velocity (mean ± SEM) of rats in the trapped condition was greater than that of control rats throughout the session. (**E**) The ratio of the average activity during the second half of sessions relative to the average activity during the first half (mean ± SEM) was greater for rats in the trapped condition on days 1 to 6 than for rats in control conditions.

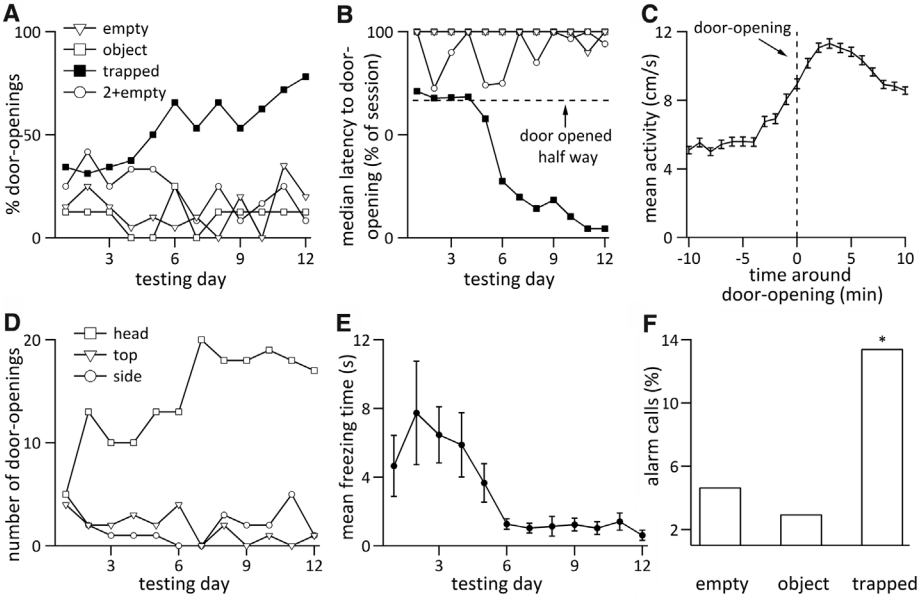

Fig. 2. (**A**) The proportion of rats in the trapped condition that opened the door increased across the days of testing. (**B**) Only rats in the trapped condition opened the door at decreasing latencies across days of testing. (**C**) Rats in the trapped condition showed a sharp increase in activity when the restrainer door was opened (time 0). (**D**) Across days, free rats in the trapped condition developed a consistent opening style, lifting the door up with their heads. (**E**) As rats learned to open the door, they stopped freezing in response to door-opening. (**F**) More alarm calls were recorded in the trapped condition ($n = 67$ sample files) than in empty ($n = 64$) or object ($n = 67$) conditions.

cage before the experiment (*11*). Animals who became openers had lower approach latencies than nonopeners ($P < 0.01$, t test), suggesting that successful opening behavior correlates with boldness scores (fig. S1). This demonstrates that individual trait differences may factor into the expression of pro-social behavior.

To determine whether anticipation of social interaction is necessary to motivate door-opening, we tested rats in a modified setup in which the trapped animal could only exit into a separate arena (separated condition, Fig. 4, A and B). Rats (12 pairs) were first exposed to the trapped condition (12 days); three rats did not open the door on any of the last 3 days and were not tested further. Next, rats were placed in the separated setup with a restrainer that was either empty (separated empty) or contained a cagemate (separated cagemate) for 29 days of testing. Finally, conditions were reversed so that rats previously in the separated cagemate condition were tested in the separated empty condition and vice versa, for 27 days. Thus, all nine rats were tested in counterbalanced order with both an empty and a full restrainer. Rats placed in the separated cagemate condition either continued or returned to opening the door at short latency as they had in the trapped condition. In contrast, when rats were placed in the separated empty condition, they stopped opening the door of the empty restrainer ($P < 0.001$, MMA, PLSD, Fig. 4, A and B). Thus, rats opened the door of a cagemate-containing restrainer but not of an empty restrainer, indicating that the expectation of social contact is not necessary for eliciting pro-social behavior.

In order to examine the relative value of liberating a trapped cagemate, we tested a cohort of rats in a cagemate versus chocolate paradigm. When given a choice, these non–food-deprived rats ate an average of >7 chocolate chips and no rat chow, indicating that they found chocolate highly palatable. The free rat was placed in an arena with two restrainers, one containing the trapped cagemate and the other containing five chocolate chips (chocolate cagemate condition, Fig. 4, C and D). As a control, one restrainer was empty while the other contained chocolate (chocolate empty condition). For rats in the chocolate cagemate condition, there was no difference in the door-opening latencies for the two restrainers during days 6 to 12 (Fig. 4C). In contrast, rats in the chocolate empty condition opened the chocolate-containing restrainer more quickly than the empty one ($P < 0.01$, t test, Fig. 4D). These results show that the value of freeing a trapped cagemate is on par with that of accessing chocolate chips. Like rats in the trapped condition, rats needed several days (5.8 ± 2.1) to learn to open the chocolate restrainer, which is evidence that door-opening was neither easy nor instinctual.

Although free rats in the chocolate cagemate condition could potentially eat all five

Fig. 3. (**A**) Females in the trapped, but not empty, condition opened the door at consistently shorter latencies than did males on days 7 to 12. (**B**) Activity was greater for females than males in the trapped, but not empty, condition.

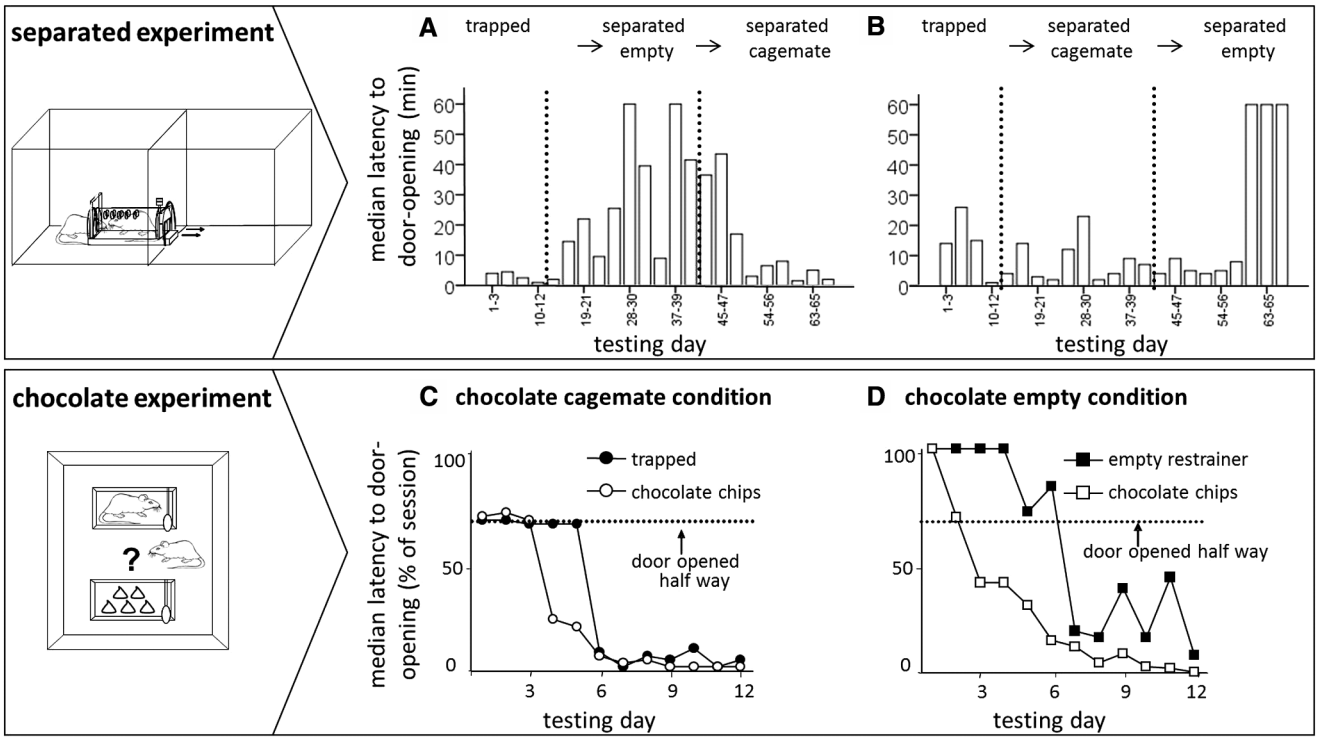

Fig. 4. (**A** and **B**) Rats opened the door for a trapped cagemate even when no social interaction was possible between the two animals after door-opening. Door-opening was extinguished when the restrainer was empty but either resumed (A) or persisted (B) when the restrainer contained a cagemate, regardless of the order of testing [$n = 4$ rats, (A); $n = 5$, (B)]. (**C**) On days 6 to 12, the latencies at which rats opened a restrainer containing a trapped cagemate and one containing chocolate chips were not different. (**D**) Rats in the chocolate empty condition opened the empty restrainer at significantly longer latencies than the chocolate restrainer.

chocolate chips, they shared them in half of all trials (52%) and in 61% of trials on days 6 to 12. Rats in the chocolate empty condition ate virtually all the chips (4.8 ± 0.7), whereas free rats in the chocolate cagemate condition ate fewer chips (3.5 ± 1.5, $P < 0.01$, t test), which allowed trapped rats to eat the remaining chips (1.5 ± 1.4).

Our study demonstrates that rats behave pro-socially when they perceive a conspecific experiencing nonpainful psychological restraint stress (*14*, *15*), acting to end that distress through deliberate action. In contrast to previous work (*5*, *9*, *16*, *17*), the present study shows pro-social behavior accomplished by the deliberate action of a rat. Moreover, this behavior occurred in the absence of training or social reward, and even when in competition with highly palatable food.

Our observations could have alternative explanations. Rats may have acted to stop the alarm calls of the trapped rats (*18*). Yet alarm calls occurred too infrequently to support this explanation. Alternatively, rats may have been attracted to the trapped cagemate by curiosity. However, door-opening in the separated cagemate condition persisted for over a month, a time period over which curiosity extinguishes (*19*). Finally, door-opening could be a coincidental effect of high activity levels. This is unlikely because once rats learned to open the door, they did so at short latency, using a consistent style, and were unsurprised by door-opening. Additionally, door-opening is not easy, rendering accidental openings unlikely. Thus, the most parsimonious interpretation of the observed helping behavior is that rats free their cagemate in order to end distress, either their own or that of the trapped rat, that is associated with the circumstances of the trapped cagemate. This emotional motivation, arguably the rodent homolog of empathy, appears to drive the pro-social behavior observed in the present study.

The presence of empathy in nonhuman animals is gaining support in the scientific community (*20*–*26*), although skeptics remain (*27*). In the current study, the free rat was not simply empathically sensitive to another rat's distress but acted intentionally to liberate a trapped conspecific. The ability to understand and actively respond to the affective state of a conspecific is crucial for an animal's successful navigation in the social arena (*4*) and ultimately benefits group survival.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/334/6061/1427/DC1
Materials and Methods
Fig. S1
Table S1
Reference (*28*)

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