

Sniffing Behavior Communicates Social Hierarchy

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Summary

Sniffing is a specialized respiratory behavior that is essential for the acquisition of odors [1–4]. Perhaps not independent of this, sniffing is commonly displayed during motivated [5–7] and social behaviors [8, 9]. No measures of sniffing among interacting animals are available, however, calling into question the utility of this behavior in the social context. From radiotelemetry recordings of nasal respiration, I found that investigation by one rat toward the facial region of a conspecific often elicits a decrease in sniffing frequency in the conspecific. This reciprocal display of sniffing was found to be dependent upon the rat's social status in two separate paradigms, with subordinates reliably decreasing their sniffing frequency upon being investigated in the face by dominant rats. Failure of subordinates to decrease their sniffing frequency shortened the latency for agonistic behavior by dominant rats, reflecting that decreases in sniffing serve as appeasement signals during social interactions. Rats rendered unable to smell persisted in displaying reciprocal sniffing behavior, demonstrating the independence of this behavior from olfaction. Oxytocin treatment in rats with established social hierarchies abolished agonistic behaviors and reciprocal sniffing displays. Together, these findings demonstrate that rodents utilize sniffing behaviors communicatively, not only to collect [6, 10–14] but also to convey information.

Results

In the present study, I measured respiration from rats during social interactions to test the role of sniffing in the context of social behaviors. Direct measures of sniffing from interacting animals have not been previously explored, because traditional tethered instruments (e.g., [6]) would become tangled during interactions. To overcome this, I adapted a head-mounted wireless transmitter system for respiration measures from interacting rat pairs. Male rats were implanted with a thermocouple into one nasal cavity to measure respiratory transients, which was fused to a chronic headplug for temporary connection to the wireless transmitter (Figure 1A). In this system, sniffing behavior of solitary and paired rats was successfully recorded concurrent with video-based measures of behavioral events, comprised of 12 distinct event types [15, 16] (see Table S1 available online). Respiratory frequency was derived from the raw nasal thermocouple signal (Figures S1A and S1B) and aligned according to the time of behavioral events to explore the possibility for distinct sniffing during these behaviors. In freely exploring rats, locomotion, rearing of the animal on its hindlimbs, and even stationary self-

directed behaviors such as grooming each corresponded with unique modulations in sniffing frequency (Figures S1C–S1E), demonstrating the reliability of video-based measures in indexing time of respiratory modulation.

In order to control the moment of the first physical interaction between rats, I used a solid black plastic divider to partition them and removed this divider after 5 min of acclimation. Upon first social interactions, sniffing behavior was characterized by highly aberrant and rapid alterations in both frequency and amplitude (Figure S1F), corresponding with periods of vigorous, bidirectional investigations directed toward the face, flank, and anogenital regions of the individual, as well as with other general exploratory behaviors (e.g., rearing). Over continued interaction, the number of social behavioral events decreased, as did sniffing frequency (Figure S1G), reflecting habituation toward the novel conspecific. I took advantage of these more quiescent epochs of paired behavior to analyze the patterns of respiration displayed by a rat upon snout investigation toward a conspecific's anogenital region, flank, and face—three areas commonly inspected during rodent social behaviors [8, 16].

Directed investigation toward either the flank or anogenital region (Figures S1H–S1J) corresponded with mean tendency to increase sniffing frequency in both the investigator and the recipient rat (Figures 1B and 1C), albeit with interanimal variability in increase magnitude (Figures 1B and 1C, right). This finding is consistent with the idea that rodents use sniffing to acquire odor information (the investigator) [4] and also display sniffing in states of arousal (the recipient) [5]. Strikingly, face investigation was commonly associated with decreases in sniffing frequency in the recipient (Figure 1D). In particular, upon being sniffed in the face, a subset of recipient rats displayed a reciprocal decrease in sniffing frequency ranging from 6.1% to 25.2% (interanimal range, 3–27 events per animal, mean \pm SD 11.1 \pm 8.1) (Figure 1D, right). Of all social encounters measured, only during face-to-face encounters did recipient rats as a population display significantly decreased sniffing frequency compared to initiating investigator rats ($p = 0.039$, $df = 17$, $n = 8$ rat pairs) (Figure 1D, right).

The stereotyped sniffing response by recipient rats during face investigation grossly resembles appeasement signals observed in other animals [17], suggesting that rats may be communicating during these epochs. Communication displays are often dictated by social status and hierarchy [18–20]. If the reciprocal display of sniffing behavior between paired rats reflects a communicative cue, then divergent social status, which is known to occur naturally between rats following continuous paired interaction [16, 21], should associate with respiratory frequency changes during these encounters. To test this, I monitored respiration across two repeated social pairings between large males (>400 g) and small males (200–300 g) and, separately, between males (>300 g) and females (200–250 g) that were ovariectomized to enhance likelihood of submissive behavior (Figures 2A and 2B). In both paradigms, large males displayed significantly greater levels of agonistic behaviors compared to their small male and/or female conspecifics (Figure S2). Supporting the hypothesis that the previously observed reciprocal sniffing behavior

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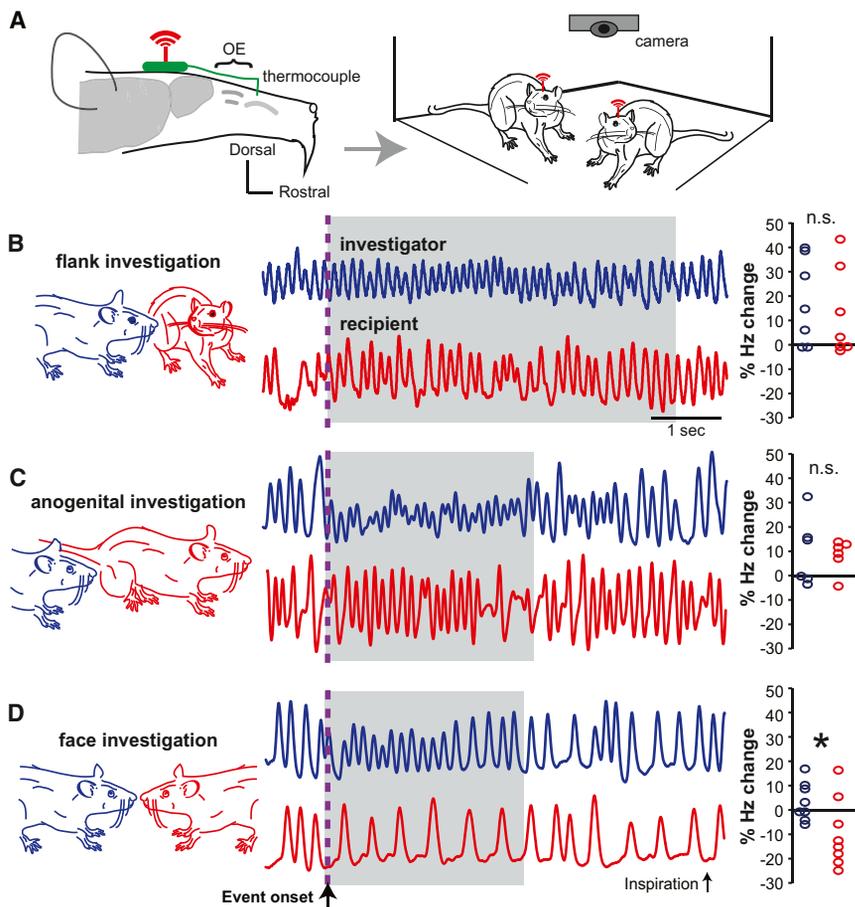


Figure 1. Rat Recipients of Face-to-Face Investigations Display Reciprocal Decreases in Respiratory Frequency

(A) Diagram of recording design, including thermocouple implanted in the nasal recess, anterior to the olfactory epithelium (OE) to access respiratory transients, and cranial plug (green) for temporary connection to wireless radio transmitter (red) during video-recorded solitary or paired behavior in an open arena (right). (B–D) Cartoons illustrating, and example traces from, paired rats during flank (B), anogenital (C), and facial investigation (D). Trace of the rat performing the investigation is blue (“investigator”); trace of the rat “recipient” of the investigation is red. Gray shaded box indicates duration of event. To the right of each example trace is the mean percent change in respiratory frequency of individual rats during performance of each investigative behavior (blue) or during receiving these investigations (red). $n = 8$ rats, 2–27 events per rat (6.7 ± 5.6 [mean \pm SD]), 1–3 sessions per rat. Not all rats contributed to each event type. % change = -1.5 – 0.5 s pre-event start versus 0.5 – 1.5 post-event start. * $p < 0.05$, investigator versus recipient, n.s. = not significant ($p > 0.05$).

they were tested for social behavior. Among subordinate rats with demonstrated anosmia (Figure 3B), reciprocal sniffing responses during face investigation persisted at levels statistically similar to baseline ($p = 0.14$, $df = 13$, $n = 7/6$ rats [baseline/ $ZnSO_4$]) (Figures 3C, 3D, and S3). This finding suggests

during face-to-face investigations is dictated by social status, in both paradigms, the animal quantified as subordinate displayed significant decreases in sniffing frequency upon receipt of facial investigation by a dominant animal (Figures 2C and S2). In contrast, dominant rats in both paradigms showed either no change or an increase in sniffing frequency when sniffed in the face by a subordinate rat (Figure 2C). Thus, reciprocal displays of sniffing behavior between rats are governed by social hierarchy.

The subordinate rat might be displaying the reduction in sniffing frequency in response to face-to-face investigation by dominant individuals, as an appeasement signal [17] in order to de-escalate the potential threat. To test this, from all male face-to-face events gathered in the social hierarchy tests above, I compared the latency for an agonistic behavior to be displayed by the dominant investigator rat in relation to the magnitude of sniffing frequency change in the subordinate rat upon facial investigation by the dominant rat. Across all rat pairs, the latency to the next agonistic behavior in the dominant male was correlated with the magnitude of the subordinate’s reciprocal sniffing response (Pearson’s correlation, $r = -0.59$, $df = 68$, $p < 0.01$) (Figure 2D).

I next treated the nasal epithelium with $ZnSO_4$ to induce temporary anosmia [22–24] for a test of whether reciprocal sniffing behavior in subordinate rats is dependent upon the transfer of odor information between animals, or possibly sharing odor stimulus space. Both dominant and subordinate rat pairs with established social hierarchies were treated with $ZnSO_4$. Twelve hours following lesion, animals were tested for anosmia (Figures 3A and 3B) and one to three hours later,

that in this context, reciprocal sniffing behavior of subordinate rats is independent of olfaction.

If reciprocal decreases in sniffing frequency in subordinate rats reflect a submissive behavior elicited in response to dominant rat investigation, reducing social hierarchy should eliminate the occurrence of reciprocal sniffing. To test this, I tested a new cohort of rats for baseline aggression and respiratory behavior following a single vehicle injection (0.9% NaCl) and then again following oxytocin treatment to enhance affiliative behavior [25, 26] (Figure 4A). Oxytocin treatment significantly reduced aggression scores of dominant rats compared to baseline measures (Figure 4B). Furthermore, previously submissive rats treated with oxytocin displayed significantly fewer reductions in sniffing frequency, if any, compared to baseline ($p = 0.017$, $df = 9$, $n = 5$ rats [5 rat pairs]) (Figures 4C and 4D). This result demonstrates that reciprocal sniffing behavior in subordinate rats is not simply an epiphenomenon displayed by some rats during facial investigation and solidifies the hypothesis that reciprocal sniffing behavior is social status dependent.

Discussion

An animal may select from a vast array of responses upon being approached by a conspecific. In part to deal with this inherent uncertainty and to facilitate effective social behaviors, animals convey intraspecific information. Intraspecific information can be emitted in a variety of species-specific formats and may include facial gestures, odor cues, physical contact, and colorations [27]. For instance, emission of a 50 kHz

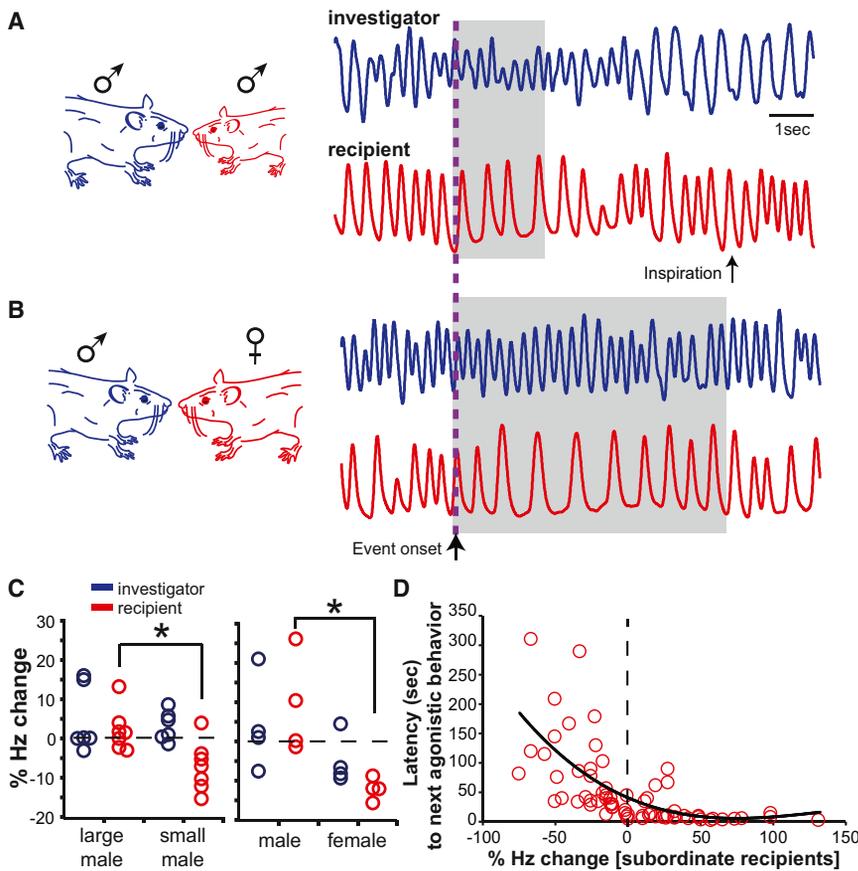


Figure 2. Reciprocal Sniffing Behavior Is Governed by Social Status and Impacts the Occurrence of Future Agonistic Behaviors

(A and B) Example traces from paired large male versus small male rats (A) and paired male versus ovariectomized female rats (B) during facial investigation. Trace of the rat performing the investigation is blue (“investigator”); trace of the rat “recipient” of the investigation is red. Gray shaded box indicates duration of event ongoing in each example.

(C) Mean percent change in respiratory frequency during face investigation (blue) or during receiving these investigations (red). $n = 6$ rat pairs (large versus small), $n = 4$ rat pairs (male versus female), 3–28 events per data point (9.1 ± 5.3 [mean \pm SD]). * $p < 0.05$, ANOVA followed by Fisher’s PLSD. Percent change = -1.5 – 0.5 s pre-event start versus 0.5 – 1.5 post-event start.

(D) Scatter plot of percent change in respiratory frequency of recipient rats as a function of latency to time of next agonistic behavior by dominant males. $n = 70$ events. Data were fit with a third-order polynomial (black line).

ultrasonic vocalization by a male rat elicits copulatory behavior from sexually receptive females [28]. In other cases, for instance the flash code that is integral to courtship and mating in fireflies, males and females actively exchange information by emitting light [29]. These and other established examples of intraspecific communication contribute to a greater understanding of animal behavior.

rapidly influence conspecific behavior in a social-status-dependent manner (Figure 4E). Whereas rodent ultrasonic vocalizations are most frequently emitted by the dominant animal, with subordinate animals displaying little ultrasonic vocalizations [30], here I found that respiratory signaling is integral to the behavioral repertoire of subordinate rats. Indeed, failure of the subordinate rats to decrease their

Direct measures of sniffing from interacting rodents have not been previously explored, despite their hypothesized critical role [8]. The present finding adds sniffing to the list of communication modalities used by rodents and reveals that, similar to ultrasonic vocalizations [28], sniffing has the capacity to

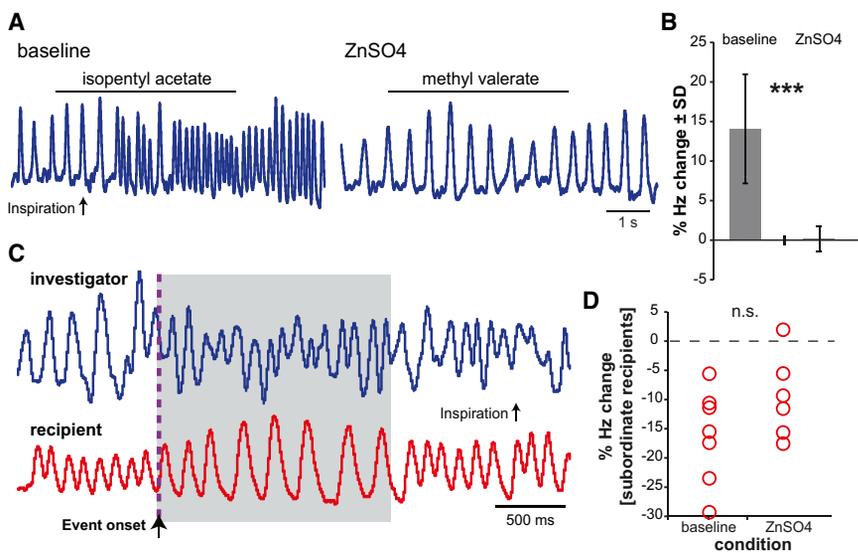


Figure 3. Reciprocal Sniffing Behavior Is Independent of Olfactory Sensory Input

(A) Example novel-odor-evoked respiratory traces from a single rat before and after ZnSO₄ treatment. Odors were presented in a counterbalanced order across all rats. Novel odors evoked an increase in respiratory frequency that was not present following ZnSO₄ treatment.

(B) Quantification of percent change in respiratory frequency to novel odors across rats before and after ZnSO₄ treatment. *** $p < 0.0001$, ANOVA followed by Fisher’s PLSD.

(C) Respiratory traces from two ZnSO₄-treated rats with established social hierarchies during face investigation. The submissive recipient rat persisted in display of reductions in respiratory frequency upon being sniffed by the dominant investigator.

(D) Percent change in respiratory frequency from anosmic (ZnSO₄-treated) rats upon being sniffed in the face. $n = 3$ – 28 events per data point (9.1 ± 5.3 [mean \pm SD]). Percent change = -1.5 – 0.5 s pre-event start versus 0.5 – 1.5 post-event start. n.s. = $p > 0.05$, ANOVA followed by Fisher’s PLSD.

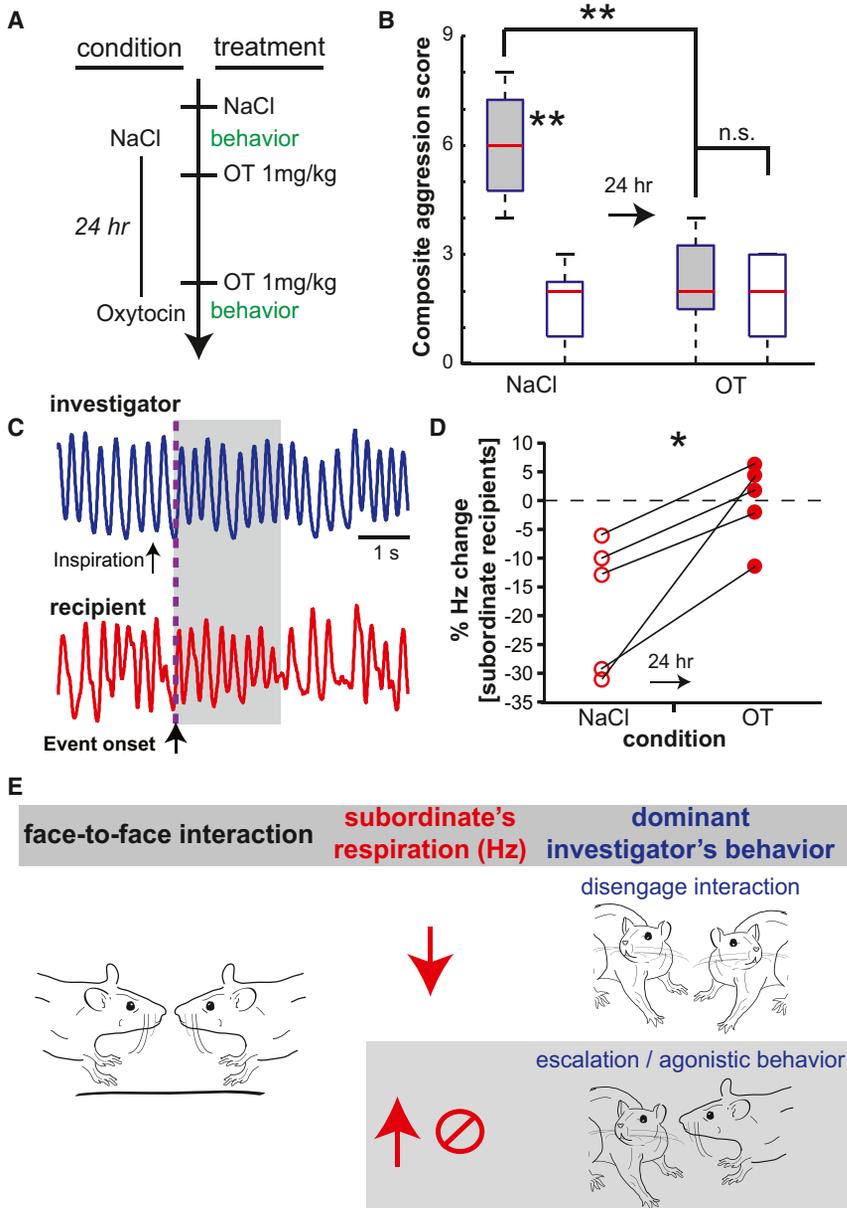


Figure 4. Oxytocin to Abolish Agonistic Behavior Eliminates the Display of Reciprocal Sniffing Behavior in Previously Subordinate Rats

(A) Timeline outlining oxytocin treatment paradigm. Rats were tested for agonistic behavior following NaCl injection in a baseline test. Both prior to and following the subsequent behavior test 24 hr later, animals were injected with oxytocin (OT).

(B) Composite aggression behavior scores from dominant (gray boxes) and subordinate (white boxes) rats. ** $p < 0.01$, n.s. = $p > 0.05$.

(C) Respiratory traces from OT-treated rats with established social hierarchies (investigator = dominant, recipient = subordinate) during face investigation.

(D) Percent change in respiratory frequency from five OT-treated subordinate rats. $n = 2-11$ events per data point (5.5 ± 2.4 [mean \pm SD]). * $p < 0.05$, ANOVA followed by Fisher's PLSD.

(E) Cartoon illustrating main finding. Upon facial investigation by a dominant rat, subordinates commonly decrease their respiratory frequency, which disengages the immediate social interaction. Failure of subordinates to decrease their respiratory frequency increases the probability of concomitant agonistic behavior by the dominant rat.

respiratory frequency shortened the latency for agonistic behavior by dominant rats. This lends an adaptive nature to the sniffing behavior observed herein. Whether changes in sniffing may serve adaptive functions in the context of other social behaviors (e.g., maternal behavior) remains to be explored.

Surprisingly, this reciprocal sniffing behavior did not require olfaction. Indeed, both the investigator rat and the recipient rat persisted in displaying changes in sniffing frequency (increases and decreases, respectively) during social interactions despite functional anosmia induced by $ZnSO_4$. Thus, the orchestration of this behavior fundamentally differs from traditionally measured agonistic behaviors in several types of rodents [31–35], which by many accounts rely upon odor input. It is likely that modulation in sniffing frequency in the contexts reported herein involves subtle changes in auditory and/or somatosensory/vibrissal cues emitted by the act of respiration during proximal interactions. Future studies to explore the

sensory channel (or channels) whereby this information is conveyed from animal to animal will be essential to a complete understanding of this new form of rodent communication behavior. It might be helpful within future studies to consider the likely possibility that reciprocal sniffing behavior coincides with other established forms of communication (ultrasonic vocalizations, odor emission) that together allow optimal intraspecific communication.

The present work opens the door to a novel analysis of rodent social behaviors by demonstrating the dual use of sniffing. Indeed, rats utilize sniffing not only to sample odors, as is well established [3, 4], but also, based upon this

work, to communicate [17]. The variation observed in sniffing behavior during social encounters suggests that this behavioral signal has the capacity to convey multiple types of information depending upon context. Investigations into this highly microstructured social behavior may be valuable in studies of neural and chemical mechanisms of social behavior.

Experimental Procedures

Detailed descriptions of all experimental procedures can be found in the [Supplemental Experimental Procedures](#).

Surgical Procedures and Animal Care

All animal procedures were in accordance with the guidelines of the National Institutes of Health and were approved by the Institutional Animal Care and Use Committee at Case Western Reserve University. Thirty-seven adult Long-Evans rats (Charles River Laboratories) were mounted into a stereotaxic frame under isoflurane anesthesia and implanted with a thermocouple (catalog number 5TC-TT-K-36-36, Omega) into the dorsal nasal recess. The thermocouple leads were then inserted into a plastic female screw-plug

adaptor (Emka Technologies) and cemented onto the skull. All female rats were ovariectomized to control for endogenous hormone fluctuations. Animals were housed singly starting the day of implantation.

Recordings

A screw-on radio frequency transmitter (Emka RodentPACK) was temporarily secured to the surgically implanted female screw-plug adaptor for access of respiratory behavior. Respiration (via intranasal thermocouple) from either solitary or paired rats was filtered 0.1–100 Hz online and digitized/stored at 500 Hz in code written in National Instruments LabVIEW.

Behavior

All behavior tests were performed in a dimly lit, well-ventilated room at 20°C–22°C in an open-top glass arena. Before any social interactions, rats were already acclimated to the head transmitter, the experimental fitting of the head transmitter to the rat, the room, and the arena.

ZnSO₄ Lesion of the Olfactory Epithelium

ZnSO₄ lesions were performed following previously published methods [22–24]. Briefly, 50 µl of 5% ZnSO₄ was administered into each nostril, and animals were allowed to recover overnight prior to further testing.

Oxytocin Treatment

To modulate affiliative behavior [25, 26, 36–38], male rats were injected with oxytocin (1 mg/kg, intraperitoneally) both 24 and 2 hr before behavior testing (Figure 4A), following established methods [39]. No rat was tested for effects of oxytocin more than once.

Stimulus Presentation

Novel odorants were presented to rats in order to test for odor-evoked orienting responses [14, 40] as a functional demonstration of ZnSO₄-induced anosmia. Odorants included isopentyl acetate and methyl valerate (Sigma-Aldrich) both at a 1:10 dilution in mineral oil.

Data Analysis

Filtered respiration data (0.1–50 Hz, second-order band pass) were peak detected in custom macros written in Visual Basic, and the time and amplitude of each peak-detected respiratory cycle were imported along with behavioral events (manually identified to the nearest 0.1 s based upon video measures) into Microsoft PowerPivot for Excel and analyzed in custom routines (<http://www.powerpivotpro.com/>). To analyze respiratory frequency within and across behavioral events, the instantaneous sniff frequency was calculated for each respiratory cycle based on the interval between a peak and the one before it [41].

Behavioral events (Table S1) were indicated in relation to each rat through offline analysis of video recordings. Aggressive behavior composite scores were calculated using established methods [16, 42–44]. The occurrences of dominance posture, anogenital investigation, kicking, and boxing (standing on hindpaws with forepaws extended to push against the conspecific) were tallied for each rat during the first 10 min of each paired behavioral session [45]. Pursuits (one rat following close to the rear of a fleeing rat for >2 s) were also recorded as agonistic behaviors but were not tallied in the aggression composite scores [44].

All statistical tests were performed in MATLAB or Microsoft Excel. *p* values were calculated by ANOVA followed by Fisher's protected least significant difference (PLSD) post hoc tests unless otherwise specified. Values are reported as mean ± SEM unless otherwise indicated.

Supplemental Information

Supplemental Information includes three figures, one table, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.02.012>.

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References

1. Welker, W.I. (1964). Analysis of sniffing in the albino rat. *Behaviour* 22, 223–244.
2. Dethier, V.G. (1987). Sniff, flick, and pulse: an appreciation of interruption. *Proc. Am. Philos. Soc.* 131, 159–176.
3. Uchida, N., Kepecs, A., and Mainen, Z.F. (2006). Seeing at a glance, smelling in a whiff: rapid forms of perceptual decision making. *Nat. Rev. Neurosci.* 7, 485–491.
4. Wachowiak, M. (2011). All in a sniff: olfaction as a model for active sensing. *Neuron* 71, 962–973.
5. Clarke, S., and Trowill, J.A. (1971). Sniffing and motivated behavior in the rat. *Physiol. Behav.* 6, 49–52.
6. Wesson, D.W., Donahou, T.N., Johnson, M.O., and Wachowiak, M. (2008). Sniffing behavior of mice during performance in odor-guided tasks. *Chem. Senses* 33, 581–596.
7. Kepecs, A., Uchida, N., and Mainen, Z.F. (2007). Rapid and precise control of sniffing during olfactory discrimination in rats. *J. Neurophysiol.* 98, 205–213.
8. Grant, E.C. (1963). An analysis of the social behaviour of the male laboratory rat. *Behaviour* 21, 260–281.
9. Doty, R.L. (1986). Odor-guided behavior in mammals. *Experientia* 42, 257–271.
10. Youngentob, S.L., Mozell, M.M., Sheehe, P.R., and Hornung, D.E. (1987). A quantitative analysis of sniffing strategies in rats performing odor detection tasks. *Physiol. Behav.* 41, 59–69.
11. Uchida, N., and Mainen, Z.F. (2003). Speed and accuracy of olfactory discrimination in the rat. *Nat. Neurosci.* 6, 1224–1229.
12. Rojas-Libano, D., and Kay, L.M. (2012). Interplay between sniffing and odorant sorptive properties in the rat. *J. Neurosci.* 32, 15577–15589.
13. Cenier, T., McGann, J.P., Tsuno, Y., Verhagen, J.V., and Wachowiak, M. (2013). Testing the sorption hypothesis in olfaction: a limited role for sniff strength in shaping primary odor representations during behavior. *J. Neurosci.* 33, 79–92.
14. Verhagen, J.V., Wesson, D.W., Netoff, T.I., White, J.A., and Wachowiak, M. (2007). Sniffing controls an adaptive filter of sensory input to the olfactory bulb. *Nat. Neurosci.* 10, 631–639.
15. Grant, E.C., and Mackintosh, J.H. (1963). A comparison of the social postures of some common laboratory rodents. *Behaviour* 21, 246–259.
16. Christie, M.H., and Barfield, R.J. (1979). Effects of castration and home cage residency on aggressive behavior in rats. *Horm. Behav.* 13, 85–91.
17. Aureli, F., Cords, M., and van Schaik, C.P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. *Anim. Behav.* 64, 325–343.
18. Nyby, J., Dizinno, G.A., and Whitney, G. (1976). Social status and ultrasonic vocalizations of male mice. *Behav. Biol.* 18, 285–289.
19. Hagedorn, M., and Heiligenberg, W. (1985). Court and spark: electric signals in the courtship and mating of gymnotid fish. *Anim. Behav.* 33, 254–265.
20. Hurst, J.L. (1990). Urine marking in populations of wild house mice *Mus domesticus* Ruddy. II. Communication between females. *Anim. Behav.* 40, 223–232.
21. Grant, E.C., and Chance, M.R.A. (1958). Rank order in caged rats. *Anim. Behav.* 6, 193–194.
22. Stewart, W.B., Greer, C.A., and Teicher, M.H. (1983). The effect of intranasal zinc sulfate treatment on odor-mediated behavior and on odor-induced metabolic activity in the olfactory bulbs of neonatal rats. *Brain Res.* 284, 247–259.
23. Mayer, A.D., and Rosenblatt, J.S. (1993). Peripheral olfactory deafferentation of the primary olfactory system in rats using ZnSO₄ nasal spray with special reference to maternal behavior. *Physiol. Behav.* 53, 587–592.
24. Alberts, J.R., and Galef, B.G., Jr. (1971). Acute anosmia in the rat: a behavioral test of a peripherally-induced olfactory deficit. *Physiol. Behav.* 6, 619–621.
25. Carter, C.S., Williams, J.R., Witt, D.M., and Insel, T.R. (1992). Oxytocin and social bonding. *Ann. N Y Acad. Sci.* 652, 204–211.
26. Keverne, E.B., and Curley, J.P. (2004). Vasopressin, oxytocin and social behaviour. *Curr. Opin. Neurobiol.* 14, 777–783.

27. Bradbury, J.W., and Vehrencamp, S.L. (2011). *Principles of Animal Communication*, Second Edition (Sunderland, MA: Sinauer Associates).
28. McIntosh, T.K., Barfield, R.J., and Geyer, L.A. (1978). Ultrasonic vocalisations facilitate sexual behaviour of female rats. *Nature* 272, 163–164.
29. Lloyd, J.E. (1971). Bioluminescent communication in insects. *Annu. Rev. Entomol.* 16, 97–122.
30. Thomas, D.A., Takahashi, L.K., and Barfield, R.J. (1983). Analysis of ultrasonic vocalizations emitted by intruders during aggressive encounters among rats (*Rattus norvegicus*). *J. Comp. Psychol.* 97, 201–206.
31. Lumia, A.R., Westervelt, M.O., and Rieder, C.A. (1975). Effects of olfactory bulb ablation and androgen on marking and agonistic behavior in male Mongolian gerbils (*Meriones unguiculatus*). *J. Comp. Physiol. Psychol.* 89, 1091–1099.
32. Edwards, D.A., Nahai, F.R., and Wright, P. (1993). Pathways linking the olfactory bulbs with the medial preoptic anterior hypothalamus are important for intermale aggression in mice. *Physiol. Behav.* 53, 611–615.
33. Wood, R.I., and Newman, S.W. (1995). Integration of chemosensory and hormonal cues is essential for mating in the male Syrian hamster. *J. Neurosci.* 15, 7261–7269.
34. Stowers, L., Holy, T.E., Meister, M., Dulac, C., and Koentges, G. (2002). Loss of sex discrimination and male-male aggression in mice deficient for TRP2. *Science* 295, 1493–1500.
35. Alberts, J.R., and Galef, B.G., Jr. (1973). Olfactory cues and movement: stimuli mediating intraspecific aggression in the wild Norway rat. *J. Comp. Physiol. Psychol.* 85, 233–242.
36. McCall, C., and Singer, T. (2012). The animal and human neuroendocrinology of social cognition, motivation and behavior. *Nat. Neurosci.* 15, 681–688.
37. Nelson, E.E., and Panksepp, J. (1998). Brain substrates of infant-mother attachment: contributions of opioids, oxytocin, and norepinephrine. *Neurosci. Biobehav. Rev.* 22, 437–452.
38. Carter, C.S. (1992). Oxytocin and sexual behavior. *Neurosci. Biobehav. Rev.* 16, 131–144.
39. Leuner, B., Caponiti, J.M., and Gould, E. (2012). Oxytocin stimulates adult neurogenesis even under conditions of stress and elevated glucocorticoids. *Hippocampus* 22, 861–868.
40. Wesson, D.W., Carey, R.M., Verhagen, J.V., and Wachowiak, M. (2008). Rapid encoding and perception of novel odors in the rat. *PLoS Biol.* 6, e82.
41. Wesson, D.W., Verhagen, J.V., and Wachowiak, M. (2009). Why sniff fast? The relationship between sniff frequency, odor discrimination, and receptor neuron activation in the rat. *J. Neurophysiol.* 101, 1089–1102.
42. Blanchard, R.J., and Blanchard, D.C. (1977). Aggressive behavior in the rat. *Behav. Biol.* 21, 197–224.
43. Trainor, B.C., Greiwe, K.M., and Nelson, R.J. (2006). Individual differences in estrogen receptor α in select brain nuclei are associated with individual differences in aggression. *Horm. Behav.* 50, 338–345.
44. Lumia, A.R., Thorner, K.M., and McGinnis, M.Y. (1994). Effects of chronically high doses of the anabolic androgenic steroid, testosterone, on intermale aggression and sexual behavior in male rats. *Physiol. Behav.* 55, 331–335.
45. Romeo, R.D., Schulz, K.M., Nelson, A.L., Menard, T.A., and Sisk, C.L. (2003). Testosterone, puberty, and the pattern of male aggression in Syrian hamsters. *Dev. Psychobiol.* 43, 102–108.