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Rats assess degree of relatedness from human odors

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Abstract

Despite widespread interest in the evolutionary implications of human olfactory communication, the mechanisms underlying human odor production are still poorly understood. Previous studies have demonstrated that human odor cues are related to variations in the major histocompatibility complex, but it is unclear whether odors are associated with overall genotypic variation. In this study, we investigated whether more closely related humans produce more similar odor cues. To assess objective odor qualities we tested odor similarity using rats in a habituation–discrimination paradigm. Rats were first habituated to a referent human odor and were then presented with two test odors obtained from individuals related in different degrees to the referent. Investigation times for each odor were compared. Because rats investigate novel odors longer than familiar odors, we were able to determine which test odor the rats perceived as more similar to the referent human odor. For six of ten odor donor families, rats investigated the odor of the less closely related individual significantly longer than that of the more closely related individual, and investigation durations were in the expected direction for all families. These results indicate that similarity of human odor cues is associated with degree of genetic relatedness, with more closely related humans producing more similar odor cues. This study supports the hypothesis that odor cues provide information regarding degree of relatedness and may thus affect a wide variety of human behaviors, including kin preferences, nepotism, and mate choice.
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1. Introduction

Kin recognition involves the evaluation of genetic relatedness, allowing individuals to be identified as kin or non-kin and, in some instances, allowing the assessment of degree of relatedness among kin classes [1–4]. Kin-recognition abilities are present in many animals, including mammals, amphibians, and invertebrates [2,3]. The process of kin recognition can comprise three components: the production of kin labels (e.g. odors, vocalizations, or plumage patterns), the perception of these labels by others, and the actions taken, if any, by the recognizer [2–4]. Growing evidence indicates that humans also can use kin recognition to identify family members and choose genetically appropriate mates [5–21]. Here we focus on the production of possible kin labels in humans, by determining whether axillary odors vary with genetic relatedness.

The two most commonly studied behaviors affected by kin recognition are nepotism and mate choice. In nepotism, close relatives are treated preferentially over distant relatives or non-kin, increasing the direct reproductive fitness of the recipient but at some cost to the actor [2]. However, actors indirectly increase their own fitness by increasing the chances that genes they share with their relatives are transmitted to the next generation [22]. Therefore, because close relatives share more genes, they should be the targets of nepotism to maximize the net inclusive fitness benefit received by the actor [22]. Higher investment in closely related individuals rather than distant kin or unrelated individuals (nepotism [2]) is apparent for many human behaviors, including food sharing [23], childcare [24], and healthcare [25].

Kin recognition is also important in mate choice, since individuals need to discriminate between kin and non-kin to prevent

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close inbreeding, which can lead to deleterious effects such as higher rates of miscarriages [13]. In addition, animals may use discrimination of distantly related kin and non-kin to avoid extreme outbreeding. Recently, research on mate choice has focused on the major histocompatibility complex (MHC), a set of highly diverse genes involved in immune functioning that, in humans and other species, maintains the highest amount of polymorphism and is also associated with the production of odorous compounds [26]. One study has suggested that mate choice is influenced by MHC type (called HLA in humans), as individuals apparently avoid marrying people that share the same MHC haplotype in a genetically isolated community [14]. Couples within this community that share the same MHC haplotype experience increased fetal loss rates, thus favoring the ability to assess degree of relatedness [15]. However, in a different isolated community, no evidence of MHC-based mate choice was found [27].

Because the MHC is also responsible for the production of odorous compounds in humans [26], researchers have examined the possibility that MHC-based mate choice may be mediated by odor cues. Females who are not on contraceptive pills and males rate the odors of individuals with whom they share fewer MHC alleles as more pleasant, and females state that these odors remind them of past boyfriends or husbands [16,17]. Contrary to the finding that humans prefer odors from others with whom they share the fewest alleles [16], more recent research has shown that females prefer the odors of males that share an intermediate number of MHC matches, specific to the inherited paternal alleles [18]. This result suggests that females may seek complementary genes rather than simply different genes in their partners, and that females might use their own cues as a basis for kin recognition [18,28].

Growing evidence supports a genetic basis for human odor production, with more related individuals producing more similar odor cues. Dogs are able to discriminate between the axillary odors of fraternal twins but not the odors of identical twins on the same diet [29,30]. Humans can match the odors of identical twins but not same-sex fraternal twins at rates better than chance [19] and can pair the odors of mothers and infants but not those of husbands and wives [20]. Mothers are better at identifying the odors of their genetic children than odors of their stepchildren, and children are better at identifying the odors of their full siblings than half-siblings or stepsiblings [21].

Although it is apparent that individuals have distinct odors and that odors differ between kin and non-kin, no study has explored the degree to which these phenotypic labels vary directly with degree of genetic relatedness. Rats can discriminate between the odors of humans with different MHC types [31] and can discriminate degrees of relatedness based on the odors of conspecifics [32]. Because of this, we used odor discrimination by rats to determine if human odors can serve as objective kinship cues for degree of relatedness.

2. General methods

2.1. Animals and housing

Adult male Sprague–Dawley rats (4–10 months old; 400–500 g) were procured from Harlan Sprague–Dawley and housed in pairs. At least one week before testing, the rats were then housed singly in 27 × 48 × 20 cm polycarbonate cages with food and water available *ad libitum* (14/10 h light/dark; lights on at 0800 h and off at 2200 h, CST).

Prior to testing, the rats received experience with olfactory habituation–discrimination tasks using chemical odors and/or odors from humans not involved in these studies to familiarize the rats to the odor presentation apparatus and habituation–discrimination tasks. In the tasks using chemical odors, rats were habituated to one chemical odor and then, in a test trial, were simultaneously presented with the referent chemical odor and a novel chemical odor to ensure that the rats investigated novel odors longer than familiar odors. In the tasks using human odors, rats were presented with a swab containing no odor and a swab containing human odor to ensure that the rats investigated swabs containing human axillary odor longer than swabs containing no odor. Results of these pilot tests are described below.

2.2. Human odor collection

Prior to odor collection, oral consent was obtained from all human participants. Individuals were told that their odors would be collected and presented to rats to determine if a link between similarity of human body odor and genetic relatedness exists. Each individual lived in a different household to avoid potential effects of shared environmental odors or diet [30]. Donors were all reproductively mature; parity, reproductive status and phase of menstrual cycle were not recorded and therefore were not controlled. Because the odor donors were not tested for genetic relatedness, degrees of relatedness were estimates based on self reports. Therefore, all coefficients of relationship (r), except for mothers and offspring, are only estimates and may not accurately reflect the actual genetic relatedness between two subjects. For mothers/offspring and for siblings, $r \approx 0.5$; for grandmothers/granddaughters and for aunts/nieces, $r \approx 0.25$; for cousins, $r \approx 0.125$; for unrelated individuals, $r \approx 0$.

On the day of odor collection, the donors refrained from eating highly odorous foods, using deodorant and other fragrance products, and smoking. Individuals showered with unscented Ivory soap that was provided by the experimenter. The donors then waited for three hours after showering and collected their odors themselves. The donors were instructed to continue with their normal daily activity during these three hours. To collect their odors, subjects swiped each underarm once with a set of either 15 or 20 cotton swabs (Puritan 15 cm cotton-tipped applicators, Hardwood Products Company, Guilford, ME). The number of cotton swabs used depended on the number of animals exposed to the human odors during the experiments. After collecting their odors, subjects placed each swab in a separate plastic freezer bag and placed the swabs in a home freezer until one of us (EMA or JMM) retrieved them less than 24 hours later. After removing most of the swab's stick, we placed each swab in a 1.5 mL microcentrifuge tube (Fisher Scientific Inc., Pittsburgh, PA) and froze them at −30 °C for later use in the experiment. Prior to odor presentation, swabs were allowed to thaw in their closed containers at room

temperature for fifteen minutes. Latex gloves were worn to prevent odor transfer to the cotton swabs.

2.3. Odor presentations and data collection

All trials were conducted in the rats' home cages. Swabs containing odors were placed in clean 1.5 mL tubes with the scented cotton ends facing out. The tubes were inserted into Teflon slots in a 10×8×10 cm stainless steel odor presentation apparatus that rested on the floor of the cage and could not be moved by the animals. The three Teflon slots were 2.5 cm apart and 6.5 cm from the bottom of the apparatus. Although the animals were able to smell the odors, they could not come into direct contact with the swabs.

The odor tests used an odor habituation–discrimination paradigm. Each rat was presented with a cotton swab containing a habituation odor that was placed in a tube in the middle slot of the odor presentation apparatus. The rats were habituated to this referent odor for four trials of 3 minutes each. The rats were then presented with two test odors. The two test odor swabs were placed in the left and right slots of the odor apparatus with the side of odor presentation balanced across rats. Test trials also lasted 3 minutes each. Investigation times of the final habituation and test odors were compared statistically.

Pilot studies indicated that rats investigate novel odors longer than familiar odors. We habituated rats to one chemical odor (either geraniol or ethyl 2-methylbutyrate) over 3 trials and tested investigation time between the habituated odor and a novel chemical odor (again, either ethyl 2-methylbutyrate or geraniol). Rats investigated the novel chemical odor significantly longer than the familiar chemical odor (two-tailed paired t test on the normal distribution, $t(4)=3.54$, $p=0.024$; mean±SEM novel: 6.40±1.17 s, familiar: 2.60±1.25 s).

All trials were videotaped from above the cages (Sony Digital8 HandyCam) so that the rat's nose and the swabs could be seen clearly. Investigation of the respective odors was scored when an animal's nose was within 0.5 cm of the odor source by an experimenter who was not blind to the hypotheses and design of the study (EMA). However, due to the length of time between running and scoring the trials (at least 2 weeks) and the randomized location of the test odors, she reported being unable to recall the respective identity of the test odors. In addition, an individual blind to the hypotheses and identity of the stimuli scored a subset (10%) of the samples and inter-rater reliability between the initial scorer and this second individual was 0.90 (intraclass correlation coefficient). Data scored by the second individual are not included in the analyses.

2.4. Human odor discrimination

After initial familiarization with the task, we then tested whether rats were capable of discriminating human odors based on degree of relatedness. Rats were tested on no more than one odor set per day to avoid habituation to the task, and all trials occurred between 1200 and 1800 h. Family odor sets were tested in the same order for each subject due to delays in obtaining samples from odor donors. We wanted to avoid freezing the samples for different lengths of time for each of the families. Although we cannot rule out subtle effects of ordering, there was no apparent trend in responding across sessions.

In pilot studies to determine that rats could smell the human odors, rats investigated swabs that had been frozen and that contained human axillary odor significantly longer than blank swabs that had also been frozen (two-tailed paired t test on the normal distribution, $t(5)=2.6$, $p=0.048$; mean±SEM human: 2.17±0.83 s, blank: 0.0±0.0 s), indicating that odor cues were preserved. For the experiments reported here, each rat was presented with a human referent odor for four 3 minute trials as described above. They were then presented with two test odors obtained from donors related in different degrees to the referent. The test-odor donors included mothers, nieces, grandmothers, aunts, sisters, and female cousins of the referents as well as individuals unrelated to the referents (see Results of Experiments 1 and 2 for details). The side of presentation for the odor from the less related individual was balanced across subjects.

We predicted that the animals in this study would investigate the odor from the individual less related to the human referent longer than the odor from the individual more related to the referent if more closely related individuals produce more similar odor cues. If degree of relatedness influences odor cue similarity, then the odor from the less related individual would be perceived as less familiar than the odor from the more related individual and would thus be investigated longer [33].

2.5. Statistical methods

Repeated-measures ANOVAs with Greenhouse–Geisser corrections and one-tailed Bonferroni post-hoc comparisons were used to evaluate comparisons of investigation duration for the final habituation trial, the odor of the more related individual, and the odor of the less related individual. For repeated-measures ANOVAs, significance levels were set at $\alpha=0.05$; for Bonferroni post-hoc comparisons, significance levels were set at $\alpha=0.033$. When necessary, data were normalized using a log $(1+x)$ transformation; normality of distributions was verified with Kolmogorov–Smirnov tests. One-tailed tests were used because, across taxonomic groups, as an animal habituates to an odor, investigation time decreases, and after habituation the animal investigates a novel odor longer than the familiar odor if a difference is perceived [33–40]. In addition, in a pilot test rats investigated novel odors significantly longer than familiar odors, supporting our *a priori* prediction that after habituation to a referent odor, an animal would investigate an odor from an individual less related to the referent longer than an odor from a more related individual because the odor from the less related individual would be less similar to the referent odor.

3. Experiment 1

3.1. Methods

Experiment 1 tested whether rats can discriminate between human odors of related and unrelated individuals. Five families

of two genetically related adult females each plus five adult females unrelated to the families were used as odor donors, for a total of fifteen females. Eight adult male Sprague–Dawley rats were used in the habituation–discrimination task. Each rat was tested with all five families in the same order.

3.2. Results

The results for the discrimination of human kin and non-kin odors in each family are presented in Fig. 1. Repeated-measures ANOVAs with Greenhouse–Geisser corrections revealed significant differences in investigation for all families (family 1: $F(2, 14)=18.18$, $p<0.001$; family 2: $F(2, 14)=12.35$, $p=0.005$; family 3: $F(2, 14)=10.93$, $p=0.006$; family 4: $F(2, 14)=19.25$, $p=0.001$; family 5: $F(2, 14)=4.96$, $p=0.043$). Bonferroni post-hoc comparisons revealed that for all families, rats investigated the odor of the unrelated individual significantly longer than the referent odor presented on the last habituation trial; for family 4 only, rats investigated the odor of the individual related to the referent significantly longer than the referent odor presented on the last habituation trial; and for families 1, 2, and 4, rats investigated the odor of the unrelated individual significantly longer than the odor of the related individual (all $p<0.033$). For families 3 and 5, investigation durations of the odors presented during the test trials were not significantly different, but were in the expected directions.

4. Experiment 2

4.1. Methods

Experiment 2 tested whether rats can discriminate among odors of human kin who differed in coefficients of relationship. Six families of three genetically related adult females were used as odor donors, for a total of eighteen females. Six adult male Sprague–Dawley rats, which were not part of Experiment 1,

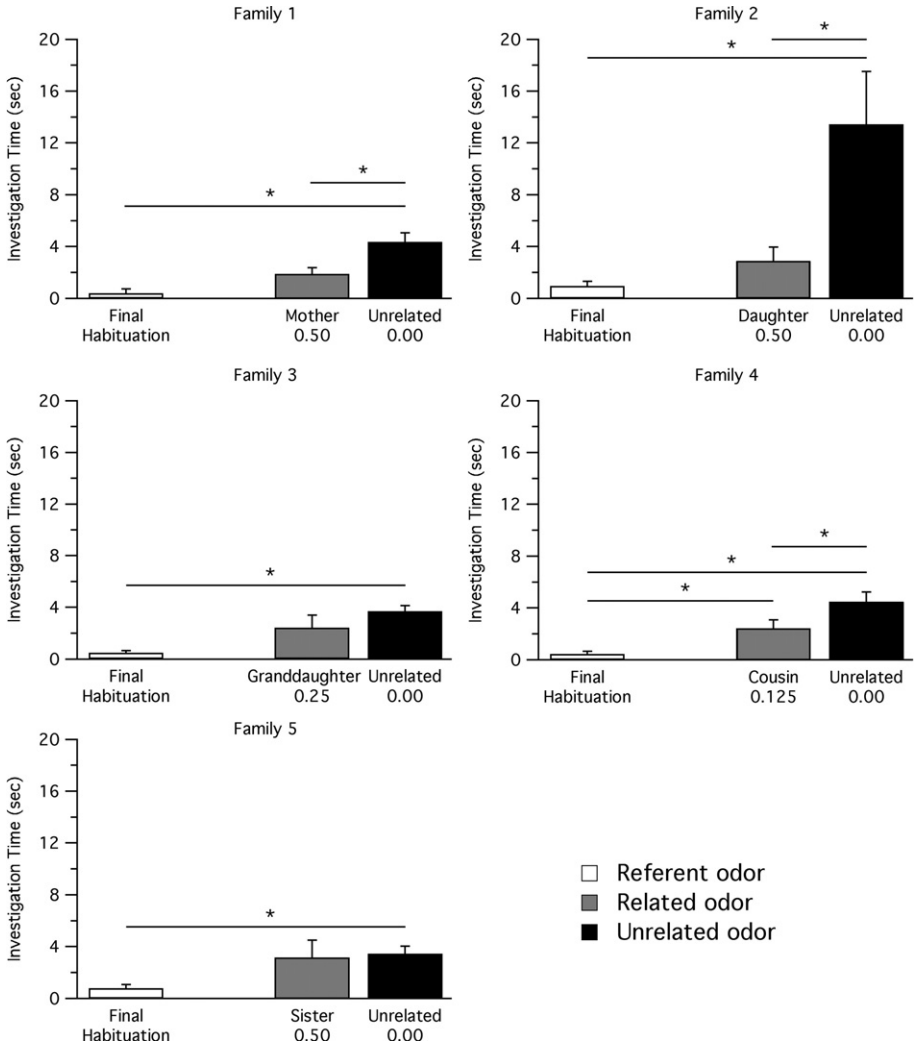

Fig. 1. Experiment 1. Duration of investigation (mean+SEM) of human kin and non-kin odors by rats in habituation–discrimination trials. Open bars represent investigation of the referent odor, gray bars represent investigation of the odor from the related individual, and black bars represent investigation of the odor from the unrelated individual. Numbers below category labels are estimated coefficients of relationship between the referent and the test odor donor. Horizontal bars and asterisks represent differences in investigation of odors (*$p<0.033$; repeated-measures ANOVAs) based on post-hoc pairwise comparisons using Bonferroni corrections.

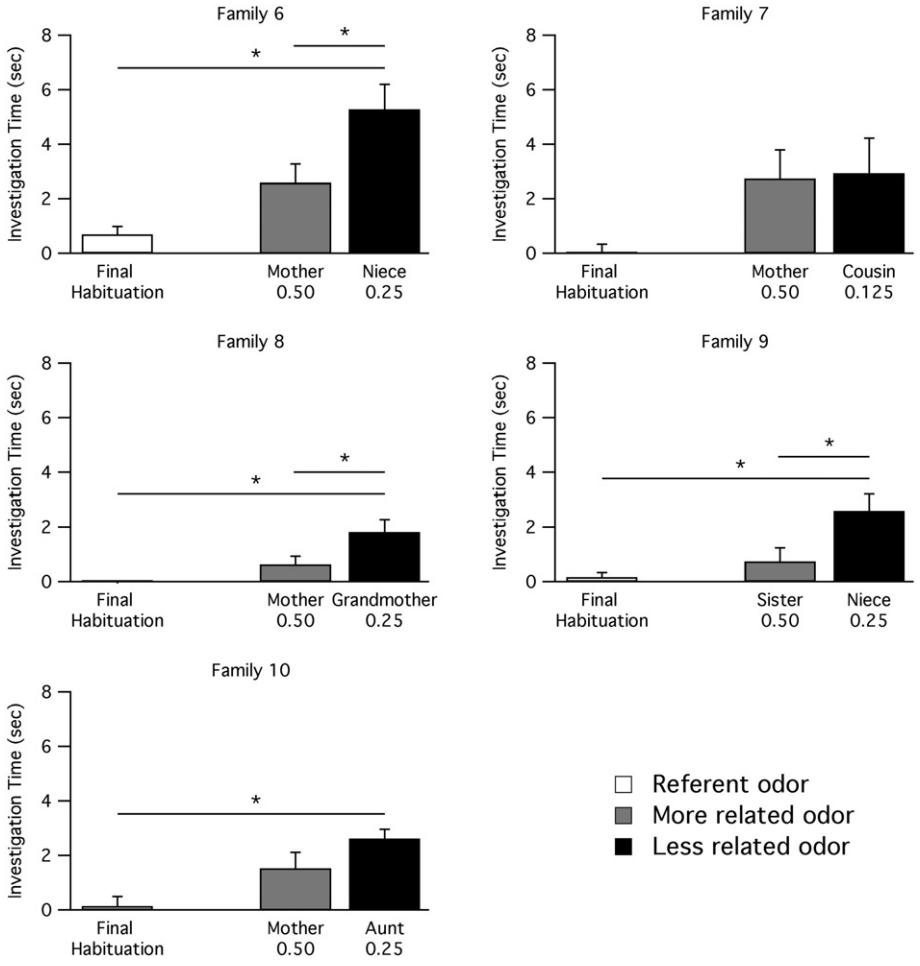

Fig. 2. Experiment 2. Duration of investigation (mean+SEM) of human kin odors by rats in habituation–discrimination trials. Open bars represent investigation of the referent odor, gray bars represent investigation of the odor from the more closely related individual, and black bars represent investigation of the odor from the less closely related individual. Numbers below category labels are estimated coefficients of relationship between the referent and the test odor donor. Horizontal bars and asterisks represent differences in investigation of odors (*$p<0.033$; repeated-measures ANOVAs) based on post-hoc pairwise comparisons using Bonferroni corrections.

were used in the habituation–discrimination task, and each rat was tested with all six families in the same order.

One family was omitted from the analysis because the family showered with Dove soap instead of Ivory soap prior to odor collection and their odors were noticeably different from the other families' odors to a human observer (EMA). In addition, after the study we were informed that one member of this family was taking oral antibiotics, which can influence body odor [41–44]. Because the antibiotics may have altered some of the odors for this family and because the scent of the soap may have masked the human odors, data from this family were omitted from analyses.

4.2. Results

The results for the discrimination of human kin odors in each family are presented in Fig. 2. Repeated-measures ANOVAs with Greenhouse–Geisser corrections revealed significant differences in investigation for families 6, 8, 9, and 10 and marginally significant differences for family 7 (family 6: $F(2, 10)=13.91$, $p=0.003$; family 7: $F(2, 10)=4.41$, $p=0.051$; family 8: $F(2, 10)=12.95$, $p=0.004$; family 9: $F(2, 10)=9.48$, $p=0.005$; family 10: $F(2, 10)=14.62$, $p=0.004$). Bonferroni post-hoc comparisons revealed that for families 6, 8, 9, and 10, rats investigated the odor of the less related individual (the odor of the individual having the lower r with the referent) significantly longer than the referent odor presented on the last habituation trial (all $p<0.033$). Rats did not investigate the odor of the individual more closely related to the referent (the odor of the individual having the higher r with the referent) significantly longer than the odor presented on the last habituation trial for any of the families (all $p>0.033$). For families 6, 8, and 9, rats investigated the odor of the less related individual significantly longer than the odor of the more related individual (all $p<0.033$). For families 7 and 10, investigation durations of the odors presented during the test trials were not significantly different, but were in the expected directions.

5. Discussion

Overall, our habituation–discrimination studies indicate that humans produce axillary odors that vary with genetic

relatedness. In Experiment 1, after habituating to a referent odor, rats investigated the odor from the individual unrelated to the referent significantly longer than the odor from the individual related to the referent (families 1, 2, and 4). For families 3 and 5, the average investigation time was higher for the unrelated individual than the related individual but not significantly so. In Experiment 2, after habituating to a referent odor, rats investigated the odor from the individual less related to the referent significantly longer than the odor from the individual more closely related to the referent (families 6, 8, and 9). For families 7 and 10, the average investigation time was higher for the less related individual than the more related individual but only a trend toward significance was apparent. Therefore, for six of ten families, rats investigated the odor of the less closely related individual significantly longer than that of the more closely related individual, and investigation durations were in the expected directions for all families.

Potential problems with odor collection may explain why some animals did not appear to discriminate between the test odors for some families. For example, one odor donor from family 5 reported that after showering and prior to odor collection she wore a sweater that she had worn for a few hours on an earlier day after using deodorant. Deodorant may have been transferred to the cotton swabs during odor collection, thus potentially altering the donor's odor and affecting discrimination between the test odors. Participants were also not screened for oral antibiotic use but, as was previously mentioned, these medications may affect odor cue production by altering the individual's bacteria [41–44]. Differences in diet may also have played a role in odor cue quality. Although we instructed the odor donors to avoid odorous foods on the day of odor collection, we did not control their diet on the day prior to odor collection. More related individuals may have more similar diets than less related individuals and, because diet may affect odor cue quality in humans [19], the rats may have investigated the odors from the less related individuals longer not based on degree of relatedness to the referent but based instead on differences in diet. However, given that all donors lived in different homes and experienced a variety of diets, it is unlikely that our results can be explained fully by diet cues.

In future studies DNA should be collected from human odor donors to assess their actual degree of relatedness to one another. Knowing the precise degree of relatedness would further support our conclusion that rats can discriminate human odors based on degree of genetic relatedness rather than some other variable that may have differed among the donors. For the families in which investigation time did not significantly differ between the two test odors, it is possible that the estimates of relatedness between the referent and the test odor donors were inaccurate. For example, although sisters on average share 50% of their genes in common, their coefficient of relationship for a given allele can actually range between 0 and 1. Thus it is theoretically possible that a sister and an unrelated individual have the same coefficient of relationship with the referent ($r=0$); if this occurs, we would not expect differences in investigation times for the two test odors. Additionally, self reports of relatedness may not be accurate because extra pair paternity rates in humans have been estimated as high as 11% [45,46]. Assessing the MHC type of the odor donors would also help determine how MHC similarity and degree of relatedness interact as well as further clarifying whether rats can discriminate human odor cues based on MHC type. Gas chromatography could also be used as a more objective measure of similarity of human odor cues. This method has been used to compare the axillary sweat of human donors and has demonstrated that chromatograms of sweat from identical twins are more similar than are chromatograms of sweat from paired non-kin [47].

Our results demonstrate that in humans, more closely related individuals produce odor cues that are objectively perceived as more similar than those of less related or unrelated individuals. Therefore humans could make use of the information in these odors to discriminate among others as a function of relatedness. Across taxonomic groups the ability to assess degree of relatedness through odor cues is an important mechanism for behaviors such as nepotism and mate choice, and our data indicate that the same might be true for humans as well.

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