Body Odor Similarity in Noncohabiting Twins

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Abstract

There is currently considerable interest in biometric approaches using human odor as a marker of disease or genetic individuality. Body odor is also thought to be used during mate choice to select genetically compatible mates. The idea that body odor reveals information about both genetic identity and genetic similarity is most readily tested by examining odor in twin pairs. However, although this idea can be traced back 130 years to Francis Galton in 1875, most studies using dogs fail to control for shared environmental effects associated with cohabitation. Here we show that odors of identical twins (but not dizygotic twins) can be matched by human sniffers at rates better than chance, even when the twins are living apart. In addition, matching frequencies for identical twin odors were not significantly different from those for duplicate odors from the same individual. These results indicate an important genetic influence on body odor and the potential for developing technologies for human odor printing in relation to underlying genotype.

Key words: disassortative, monozygotic, odor, odour, olfaction, scent, smell

Introduction

Evidence suggests that human twins have extremely similar body odor. This idea can be traced back 130 years to Francis Galton (1875), who, in a wide-ranging essay on environmental and genetic effects on twin similarity, wrote that "it would be an interesting experiment for twins who were closely alike, to try how far dogs could distinguish between them by scent" (p. 569). We are aware of three studies that have attempted to do this. In the first, Kalmus (1955) found some evidence that dogs could discriminate between odors of identical twins in a tracking task. However, when presented with a retrieval task for the axillary odor of one twin, dogs would accept the odor of his or her identical twin, suggesting that the odors are qualitatively and perceptually similar. More recently, Hepper (1988) showed that dogs could discriminate twins provided they differed in either genetic relatedness or environmental factors but not in twin pairs identical in both factors. Finally, Sommerville et al. (1990) presented evidence that odors of twins were matched by dogs at rates greater than odors of unrelated individuals, again suggesting qualitative similarity in twin odors (see also Sommerville et al., 1994).

Here we test whether human sniffers can similarly match odors from pairs of twins. This question is interesting, partly as a comparison between two very different species, and par-

ticularly in a more functional sense in relation to humans as adaptive receivers of the olfactory information potentially available in body odor. For example, it is thought that body odor carries cues of genetic similarity, which may be used in mate selection (Wedekind et al., 1995; Wedekind and Furi, 1997) and various types of individual or kin recognition (Weisfeld et al., 2003), in common with a substantial literature in animals (e.g., Bateson, 1978; Hepper, 1986; Penn, 2002; Roberts and Gosling, 2003). In this study, we use a matching-to-sample experimental design to compare the rates of correct matching for sniffers presented with (1) monozygotic (MZ) twin pairs, (2) dizygotic (DZ) twin pairs, and (3) duplicate odor samples from the same individual. This latter test provides a background matching rate which estimates the likely maximum for human sniffers in the conditions used against which the twin matching rates could be compared.

A critical problem with two of the three dog studies described earlier (Kalmus, 1955; Sommerville *et al.*, 1990) is that they failed to control for confounding environmental effects, particularly those associated with cohabitation. Three of four twin pairs in Kalmus' experiments, and at least one of two pairs in the chemical study of Sommerville *et al.* (1994), lived together. Perception of odor similarity across twin pairs in these studies could therefore result from shared environmental factors rather than direct genetic effects. Environmental influences on individual odors are well known and include effects of diet (Beauchamp, 1976; Ferkin et al., 1997), disease (Penn et al., 1998a; Yamazaki et al., 2002; Beauchamp and Yamazaki, 2003), parasitic infection (Kavaliers and Colwell, 1995; Klein et al., 1999; Penn and Potts, 1998), and social (Novotny et al., 1990; Moore et al., 1997) or reproductive (Singh and Bronstad, 2001) status. These environmental contributions are perceived by conspecifics and influence behavioral responses to the individuals who produce the odor, notably during mate or competitor assessment (Gosling and Roberts, 2001; Beauchamp and Yamazaki, 2003, 2005). While dietary influences are likely to be most relevant in humans, any environmental influences arising from cohabitation could potentially confound any putative odor similarity determined by genetic effects. We avoided this problem by specifically selecting 32 noncohabiting twin pairs, half of which were MZ and half DZ twins.

Materials and methods

Odor collection

We collected axillary odors on cotton pads worn overnight in the twins' own homes and delivered to us by hand the following morning. All twins were female white Europeans aged 26-46 (mean = 37) and recruited from the TwinsUK adult twin registry (http://www.twinsuk.ac.uk). Zygosity was determined by a standard questionnaire and by genotyping in cases of uncertainty (Martin and Martin, 1975), as is standard for other twin studies (e.g., Mohammed et al., 2005). Each twin lived in a different household from their cotwin. We used female twins because they were available to us as part of a larger study. Female body odors may be more variable than those of males as a result of menstrual cycle influences (Singh and Bronstad, 2001; Kuukasjärvi et al., 2004). We could not control for this, but this means our results are conservative with respect to the observed rates of matching twin odors: matching rates might have been improved had we used male odors. Axillary pads were collected from all participants on the same day, in sealed plastic bags, and kept at 4°C until storage at -85°C approximately 14 h later. Pads (Premium cosmetic pads, Boots, http://www.boots.com) were 100% cotton, elliptical in shape, and approximately 9×7 cm at their longest axes, held in place using Micropore surgical tape (Boots). We prescribed a strict hygiene regime for the 24 h before sampling to ensure that axillary odors were not influenced by potential confounding factors. This regime included abstinence from perfumed products, use of a provided nonperfumed soap (Simple), wearing a cotton T-shirt prewashed in nonperfumed detergent (Surcare) over the pads, and avoidance of tobacco smoke and certain strong foods that could potentially influence odors (garlic, chilli, pepperoni, curry, strong herbs and spices, blue cheese, cabbage, asparagus, yoghurt, and fried onion). Twins were instructed to shower, attach the pads, and put on the T-shirt over the pads immediately before they went to bed and to remove the pads immediately after rising, so that most pads would have been worn for between 6-9 h.

Odor bioassays

We tested odor similarity using a matching-to-sample experimental design (Porter et al., 1985). Sniffers (members of the public at the Newcastle University Medical School and the Life Science Centre) were asked to match one odor (the sample) with one of four others (the alternatives), where the sample and one of the four alternatives were different individuals from the same twin pair and the other three alternatives were unrelated individuals from other twin pairs. The proportion of correct matches was then compared with the proportion expected by chance (0.25) using binomial tests. Halved pads were presented 1-3 h after removal from the freezer, in 500ml conical flasks with aluminum foil stoppers. We used eight flasks for each MZ or DZ odor set, of which three were not used and hidden from view for any given sniffer. Flasks were rotated between every sniffer so that each pair was used approximately equally and each flask used approximately equally as sample or alternative. Flasks were coded to prevent sniffers from guessing the correct answer. A total of 113 different sniffers completed the task both for one of the four MZ and one of the four DZ odor sets (order of presentation was alternated between sniffers). Sniffers were instructed to complete the task in their own time and told they could smell any of the flasks as often as they wished. No more than 30 sniffers were used per odor set in order to avoid any potential bias from an unusually distinctive set. To check that results were not biased in this way, we carried out reliability analyses by repeating analyses after omitting each set in turn. Results remained significant for MZ pairs in all cases (P = 0.001 - 0.025; Table 1).

For matching-to-sample tests of duplicate odors from the same individual, we randomly selected one twin from each MZ pair used in the tests described earlier, so that we had four unrelated individuals in each set (four sets). The pairs from which individuals were selected were maintained within the same set of four used in the first MZ comparison, thus controlling for potential variation in distinctiveness of odors across the two tests. For a given sniffer, we then presented one half pad from one of these four individuals as the sample and the other half as one of the four alternatives, along with halved pads from the other three individuals in the set. As before, flasks were rotated between every sniffer so that each individual was used approximately equally within each set and each flask used approximately equally as sample or alternative. A total of 120 different sniffers (different from the twin matching test) completed this task. Reliability analyses again showed that results were not biased by an especially

Analysis	MZ				DZ				Duplicate			
	m	n	Proportion	Р	m	n	Proportion	Р	m	п	Proportion	Р
All	42	113	0.37	0.003	35	113	0.31	0.089	49	120	0.41	<0.001
Less set 1	29	83	0.35	0.028	23	83	0.28	0.323	37	90	0.41	0.001
Less set 2	30	84	0.36	0.019	30	84	0.36	0.019	37	90	0.41	0.001
Less set 3	35	89	0.39	0.002	29	89	0.33	0.066	37	90	0.41	0.001
Less set 4	32	83	0.39	0.004	23	83	0.28	0.323	36	90	0.40	0.001
Males	16	44	0.36	0.063	15	44	0.34	0.114	18	41	0.44	0.006
Females	26	69	0.38	0.013	20	69	0.29	0.261	31	79	0.39	0.004

Table 1 Number of correct matches (*m*) by sniffers in matching-to-sample tests using odors from MZ and DZ twin pairs and duplicate odors from the same individual

Proportions of sniffers making the correct choice are tested from chance (0.25) using binomial tests. Sensitivity analyses are also shown, being the entire data set less one of the four odor sets in turn.

distinctive set of odors (P < 0.001 in all cases). To compare matching frequencies for MZ and DZ twins against identical odors (taking into account sniffer inaccuracy), we used binomial tests with the expected frequency set to that obtained by matching odors from the same individual (0.408).

Sniffers in all tests were recruited from members of the public, and we did not apply any screening on participation except that they should be aged 12 or over (so that we could be sure they understood the task). Restricting our sample of sniffers, for example, by including only individuals with a good sense of smell, who did not smoke or who were in good health, might have improved the frequency of matching that we recorded; our results illustrate the frequency recorded in the general population. However, to investigate some underlying aspects of sniffer sensitivity and performance, we recorded sex and age of sniffers in the duplicate odor matching tests.

Analyses

As described earlier, we compared observed frequencies of correct twin odor matching with either that expected by chance (0.25, twin matching task) or with that obtained in the duplicate odor task (0.408). These analyses were carried out using binomial tests in SPSS version 12. The binomial function in SPSS uses z score approximation in calculating probabilities and returns the likelihood of obtaining a value equal to, or more extreme than, that observed (see also Siegel and Castellan, 1988). We used one-tailed tests as we expected relatedness to increase odor similarity or to have no effect, but not to reduce it.

Results

We found that 42 of the 113 sniffers correctly matched odors of MZ twins (Table 1), which was a higher proportion (mean, 95% confidence intervals (CI): 0.37, 0.28-0.47) than expected by chance (0.25; binomial test, P = 0.003; Figure 1). The pro-

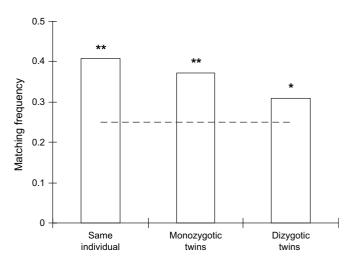


Figure 1 Proportion of correct responses by smellers tasked to match duplicate odors from the same individual (n = 120 sniffers) or from MZ or DZ twin pairs (n = 113 sniffers). Asterisks denote probabilities in binomial tests against frequency expected by chance (0.25, dotted line): *P < 0.1, **P < 0.01.

portion of sniffers who correctly matched DZ twin pairs (35/113; 0.31, 0.23-0.40) was lower than for MZ pairs, though not significantly so (tested against the frequency for MZ matching, 0.372; P = 0.101) and not significantly better than chance (P = 0.089).

Although these results suggest a discriminable genetic component to individual human odors, supporting Galton's (1875) assertion that odors of twins should be qualitatively similar, matching frequencies were generally low. Error in this task can be divided between either poor discrimination on the part of the sniffers or real odor dissimilarity between twins caused by environmental differences such as current diet or health. To estimate the strength of the contribution of these factors, we separately measured matching frequencies when the sample and one alternative were odor samples from the same axilla of the same person (using samples from one twin from the same MZ pairs as tested before). This test thus measured the frequency with which sniffers (n = 120)correctly match two identical odor samples (duplicates). The proportion of correct matches for this test was 0.41 (49/120; 95% CI: 0.32–0.50). This is again significantly better than chance (P < 0.001) but demonstrates that most sniffers match incorrectly. This test thus provides a refined baseline against which to assess frequency of odor matching across pairs of twins, which takes into account the amount of sniffer inaccuracy. We therefore compared the frequency of successful matching for the twin odors against the expected frequency for duplicates (0.408). We found that the matching frequency for odors of DZ twins was significantly lower than that found for duplicate odors (binomial test, P = 0.020), but there was no significant difference between the frequency of successfully matching MZ twins and duplicate odors (P = 0.246).

Comparing the frequencies of correct matching in the duplicate odor tests, we found no detectable effect of the gender of sniffers on task performance (data from Table 1, males 49 correct matches out of 129 tests; females 77/217; $\chi^2 = 0.218$, P = 0.64). However, we did notice an effect of age on performance in the duplicate odor task. Overall, the mean age of correct responders was 32.08 years (±SE = 1.91, n = 49), while the mean age of incorrect responders was 38.32 (±1.46, n = 71), and this difference was significant (two-tailed Wilcoxon rank-sum test, z = 3.40, P = 0.001). This result was present in both males (Figure 2; correct responders = 30.17 ± 2.46, n = 18; incorrect = 40.87 ± 2.78, n = 23; z = 3.09, P = 0.002) and females (correct = 33.19 ± 2.67, n = 31; incorrect = 37.10 ± 1.70, n = 48; z = 2.04, P = 0.041).

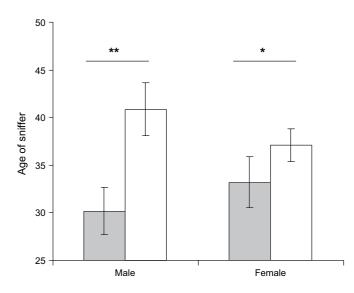


Figure 2 Mean age of male and female sniffers correctly matching duplicate odor samples in matching-to-sample tests. Asterisks denote probabilities in Wilcoxon rank-sum tests: *P < 0.05, **P < 0.01.

Discussion

Our results indicate that odor similarity in pairs of twins can be perceived by the human nose. Odors of twins are more similar to each other than they are to other individuals, as perceived by human olfaction, but only if they are identical. Matching of MZ odors occurred at rates better than chance and was not significantly different than the matching rates of duplicate odors from the same individual. This suggests that MZ twins are perceived approximately as similar as two odors from the same individual. If this result were simply due to the common rearing environment of twins, then matching of DZ twin pairs should occur at the same rate. Unlike MZ twins, however, the rate of matching DZ twins was not significantly above chance levels and was significantly lower than matching duplicate odors from the same individual. The matching rate of DZ twins was lower, but not significantly different, than the matching rate of MZ twins. Thus, the weight of the evidence indicates that MZ twin pairs smell more similar to each other than to other individuals and more similar than across DZ twin pairs, providing evidence for a genetic influence on human body odor. However, because the latter difference was not significant, we cannot completely rule out the possibility that the similarity of the twins was due to common rearing environment.

The similarity of the odor of MZ twins cannot be due to cohabitation, thus indicating a genetic explanation. While some previous studies using twin odors (Kalmus, 1955; Wallace, 1977; Sommerville et al., 1990) have certainly indicated such a genetic effect, they have not overtly selected individuals living apart, introducing the potentially confounding effect of shared environment on personal odors (Wallace used two MZ twin pairs, but no information was provided about cohabitation). Similarly, studies examining the effects of familial relatedness on odor similarity and odor recognition may often be confounded by the same problem, even though they impose rigorous hygiene regimes similar to that used here (e.g., Porter et al., 1985; Weisfeld et al., 2003). Such studies include odor recognition between mothers and offspring (Porter et al., 1983; Russell et al., 1983; Weisfeld et al., 2003), odor recognition between siblings (Porter and Moore, 1981; Weisfeld et al., 2003), and odor discrimination between different family members and familiar or unfamiliar strangers (Weisfeld et al., 2003). Furthermore, studies investigating discrimination of self or spouse odor from that of unrelated individuals (Russell, 1976; Hold and Schleidt, 1977) cannot distinguish between environmental and genetic contributions to individual odors. To date, perhaps the most convincing evidence for genetic influences on odor similarity comes from Hepper's (1988) study using dogs, in which three experiments systematically varied genetic relatedness (i.e., identical or nonidentical) and shared environments. Our study follows the approach used in Hepper's second experiment, which examined the discrimination of odors from noncohabiting adult (male) twins. It thus provides the first evidence for

human perception of odor similarity from a large sample of twins, who have been specifically selected on the basis of noncohabitation. This feature of our subject selection is critical because it incorporates a level of environmental variability between individuals, which approximates that found between two nonrelated people.

It is possible that gene-environment interactions could partially explain odor similarity within twins, despite their noncohabitation. For example, twins have a tendency to eat similar types of foods (Fabsitz et al., 1978), and a previous study comparing one twin pair on the same or different diet showed that it is harder to discriminate odors of twins on the same diet (Wallace, 1977). We reduced the likelihood of common diet influencing common odors as far as possible by our instructions to avoid strong smelling foods. However, even if they do share a tendency towards similar foods, it is improbable that all twins ate identical diets in their separate households over the days immediately preceding odor collection. Indeed, there is likely to be a multitude of such environmental differences between separate households, each of which would be expected to incrementally reduce odor similarity. Furthermore, the finding of Porter et al. (1985) that odors of cohabiting husbands and wives cannot be reliably matched by others suggests that even completely shared environmental factors are insufficient in themselves to explain perceived odor similarity in our experiments. Thus, while we cannot discount such gene-environment interactions entirely, the finding that MZ twins are matched at rates better than chance, and not significantly lower than for duplicates of the same individual, suggests an underlying genetic signature.

Possible sources of this effect are genes within or linked to the major histocompatibility complex (MHC). Although this requires further research, MHC genes appear to influence odor preferences in many vertebrate species (Penn, 2002; Bernatchez and Landry, 2003; Roberts and Gosling, 2003) including humans (Yamazaki et al., 1976; Wedekind et al., 1995; Jacob et al., 2002; Beauchamp and Yamazaki, 2005). Our results provide additional evidence that humans can detect these individual and apparently genetically determined odors. Indeed, the fact that the genetic component appears robust to a variety of environmental differences is testament to the role of odors in communicating individuality and genetic information in social interactions such as mate choice (Johnston et al., 1993; Penn and Potts, 1998b; Gosling and Roberts, 2001; Schaefer et al., 2002; Beauchamp and Yamazaki, 2003; Roberts and Gosling, 2003). This quality is also crucial to the successful development of applications using human odors, such as forensic investigation (Natale et al., 2000) and potentially in noninvasive disease diagnostics (Penn and Potts, 1998a; Mantini et al., 2000; Pavlou and Turner, 2000; Turner and Magan, 2004). Our results thus add weight to growing evidence for an important genetic influence on human body odor and indicate the potential for developing technologies for human odor printing in relation to underlying genotype.

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