

# Olfactory Functioning and Cognitive Abilities: A Twin Study

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**A Swedish version of the *National Geographic Smell Survey* (Wysocki & Gilbert, 1989) was completed by 227 twin pairs from the Swedish Adoption/Twin Study of Aging. Twins ranged in age from 45 to 89 years. Quantitative genetic analysis of four measures of olfactory functioning indicated moderate heritability for odor identification and perceived intensity and nonsignificant heritability for odor detection and perceived pleasantness. Bivariate analyses revealed that the relationship between odor identification and measures of verbal ability was primarily genetically mediated. The results provided further support for the hypothesis that odor identification and verbal ability in general tap the same cognitive domain (Larsson, 1997).**

**M**OST research in cognitive psychology has concentrated on visual and, to some extent, auditory presentation of information. Over the past decade, however, a growing body of research has focused on the perceptual and cognitive components of the sense of smell. Individuals differ in their ability to detect odors (Van Toller, Dodd, & Billing, 1985; Wysocki & Gilbert, 1989) and to identify or label odors (Russell et al, 1993; Schemper, Voss, & Cain, 1981). Furthermore, there are significant age differences in these abilities, as well as in recognition memory for odors over various delay intervals (for a review, see Larsson, 1997). The nature of these individual differences and age differences has yet to be explained. The primary objective of the present investigation was to apply quantitative genetic methods to individual differences in olfactory functioning in a sample of healthy older adults.

## *Olfactory Functioning*

One method for investigating individual differences in various olfactory functions is the twin study. Comparing the similarity of monozygotic (MZ) and dizygotic (DZ) pairs allows researchers to determine the extent to which the variance in a trait (e.g., odor detection) arises from genetic or environmental factors. Previous twin studies of olfactory functioning have focused primarily on detection of individual odors. Several twin and family studies have demonstrated a genetic basis for specific anosmias, the inability to detect a certain odor (Amoore & Steinle, 1991; Whissell-Buechy & Amoore, 1973; Wysocki & Beauchamp, 1984, 1991). For example, Wysocki and Beauchamp (1991) demonstrated that the specific anosmia to androstenone, a steroid metabolite produced by many mammals, has a significant genetic component.

In contrast, few twin studies have investigated genetic and environmental influences on variation in olfactory functioning in the normal range. Hubert, Fabsitz, Feinleib, and

Brown (1980) found no evidence for heritability of olfactory sensitivity to three odorants: acetic acid (pungent), isobutric acid (sweaty), and cyclohexanone (camphoraceous). Although MZ correlations were not significantly greater than DZ correlations for any of the odorants, the data for acetic acid were suggestive. Using a different set of odorants, Gross-Isseroff, Ophir, Bartana, Voet, and Lancet (1992) found significantly greater MZ than DZ similarity for androstenone and isoamyl acetate (banana) but not for citral (lemon) or eugenol (cloves). Finally, Segal, Topolski, Wilson, Brown, and Araki (1995) reported no difference in MZ and DZ twin correlations for detection of a single odorant (phenyl ethyl alcohol). Thus, the evidence for genetic and environmental influences on odor detection is inconsistent across odorants.

Measures of odor detection (can you smell it?) principally reflect sensory processes, whereas measures of odor identification (what is it?) reflect both sensory and cognitive processes (Wijk & Cain, 1994). In an important departure from previous investigations, Segal and colleagues (1995) also reported twin correlations for performance on an odor identification task. Segal and her colleagues administered the University of Pennsylvania Smell Identification Test (UPSIT) to 45 MZ pairs and 37 DZ pairs ranging in age from 11 to 83 years. The UPSIT is a standardized test of odor identification that requires participants to label 40 odorants presented in a multiple-choice format (Doty, Shaman, & Dann, 1984). The MZ correlation of .31 was not significantly greater than the DZ correlation of .15; however, the results are suggestive of a genetic contribution to odor identification.

One advantage of scales like the UPSIT is the increase in reliable variance that results from summing performance across several items. In a twin study, the result is increased power to detect genetic influences. Previous twin studies of odor detection have produced results that vary widely;

therefore, in the present investigation we chose to summarize responses across six odorants to create scales. The first goal of the investigation was to examine genetic and environmental contributions to individual differences on four measures of olfactory functioning: odor detection, odor identification, perceived pleasantness, and perceived intensity of the olfactory information. Perception of pleasantness and intensity are classic components of investigations of olfactory functioning (e.g., Doty, Orndorff, Leyden, & Kligman, 1978; Jones, Roberts, & Holman, 1978; Wysocki & Gilbert, 1989); however, to date these variables have not been included in a twin study of olfactory functioning.

### *Relationship With Cognitive Abilities*

Odor identification marks the point at which the bottom-up process of sensory functioning and the top-down process of cognitive abilities intersect (Richardson & Zucco, 1989). According to Schab (1991), odor identification is a semantic memory task: The participant is required to access the appropriate label for the odorant. In contrast, odor recognition taps episodic memory: Participants are presented with a set of odorants and later asked to decide which test odorants were presented before. Investigations of odor recognition memory grew out of an interest in the ability of certain odors to evoke vivid memories. Marked age differences in episodic odor recognition memory have been demonstrated (Larsson, 1997). Evidence has suggested that the age differences in odor recognition result in large part from age differences in cognitive abilities, specifically semantic memory. In two separate studies, Larsson and Bäckman (1993, 1997) demonstrated that age-related differences in odor recognition memory were eliminated when odor identification (a semantic memory task) was statistically controlled.

Odor identification may play a fundamental role in olfactory functioning and odor memory. Little evidence exists, however, about the relationship between odor identification and measures of cognitive abilities. Research has indicated that sensory deficits alone cannot explain age differences in odor identification (Larsson & Bäckman, 1993, 1997; Murphy, Cain, Gilmore, & Skinner, 1991). For example, even after screening participants to ensure equivalent performance on measures of odor sensitivity, Schemper and colleagues (1981) still found age differences in the ability to identify a set of 40 odorants. Consequently, cognitive factors must play a role (Richardson & Zucco, 1989; Schab, 1991). Larsson, Finkel, and Pedersen (2000) reported significant correlations between odor identification and cognitive abilities—particularly those cognitive measures with a strong verbal component.

The second goal of the present investigation was an examination of the nature of the relationship between odor identification and cognitive abilities. In the present analysis, quantitative genetic methods were used to determine the relative contribution of age, genes, and environments to the relationship between olfactory functioning and cognition. The correlation could arise from a variety of genetic and environmental influences. If, for example, the genetic influences on odor identification and cognition were correlated, one could conclude that the association arises through a genetically influenced mechanism, such as that influencing verbal

functioning. If, however, only the environmental influences on odor identification and cognition were correlated, this would suggest that something in the environment had produced the relationship. The environmental effect could be shared by family members, for example, when parents provide an intellectually stimulating rearing. In contrast, the environmental effect could be specific to an individual, such as lifestyle variables or a neurological trauma affecting both odor identification and cognitive ability. Thus, not only the existence of the relationship between odor identification and cognition but also potential mechanisms producing this relationship can be investigated. Understanding the nature of the correlation between odor identification and cognition will improve understanding of the nature of age differences in olfactory functioning.

In sum, our goals in the present investigation were twofold. First, we used univariate quantitative genetic analysis to determine genetic and environmental influences on four measures of olfactory functioning. Second, we used bivariate quantitative genetic analysis to determine the contributions of age, genes, and environment to the correlation between olfactory functioning and cognitive measures. To address these goals, data from the Swedish Adoption/Twin Study of Aging (SATSA; Pedersen et al., 1991) were analyzed. A Swedish version of the *National Geographic* Smell Survey (Wysocki & Gilbert, 1989) was completed by 227 twin pairs ranging in age from 45 to 89 years.

## **METHODS**

### *Participants*

Ascertainment procedures for SATSA have been described previously (Pedersen et al., 1991). In brief, the sample is a subset of twins from the population-based Swedish Twin Registry (Cederlöf & Lorich, 1978). The base population of twins consists of all pairs of twins who indicated that they had been separated before the age of 11 and reared apart and a sample of twins reared together, matched on the basis of gender and date and county of birth (Pedersen, Friberg, Floderus-Myrhed, McClearn, & Plomin, 1984). Although twins were labeled *reared apart* if they were separated by age 11, the distribution of age at separation is highly skewed. Fifty-two percent of the reared-apart twins were separated before age 1 year, 69% by age 2 years, and 82% by age 5 years (Pedersen et al., 1991). Pedersen, Plomin, Nesselroade, and McClearn (1992) found little or no effect of either age of separation or correlated rearing environments on twin similarity for cognitive abilities for the reared-apart SATSA twins. Twins were first mailed questionnaires, and a sample of those pairs in which both twins responded was invited to participate in an examination of cognitive abilities, which occurred in person. In-person testing took place in a location convenient to the twins, such as district nurses' offices, health-care schools, and long-term care clinics (Pedersen et al., 1991). Testing was completed during a 4-hr visit that involved cognitive testing and a health examination.

Demographic characteristics of the sample for the present analyses are presented in Table 1. Zygosity was determined on the basis of serological assay. The sample included 31

pairs of monozygotic twins reared apart (MZA), 55 pairs of monozygotic twins reared together (MZT), 72 pairs of dizygotic twins reared apart (DZA), and 69 pairs of dizygotic twins reared together (DZT). Participants ranged in age from 45 to 89 years. There were significant differences in the gender distribution between zygosity groups,  $\chi^2(3, N = 454) = 9.98, p < .05$ . With the exception of DZA pairs, approximately half the respondents were women. With 68% female pairs, the gender distribution of DZA pairs more nearly matched the demographic characteristics of this age range. Education was rated on a 4-point scale, and the average education score fell between 1 and 2, where 1 indicated completion of elementary education and 2 indicated completion of vocational high school. Participants were asked to rate their general health on a scale ranging from 1 (good) to 3 (bad). Use of cigarettes, cigars, and pipes was included in the calculation of packyears (Kendler, Karkowski, & Pedersen, 1999). Cigars and pipes were converted to cigarette equivalents (e.g., 1 cigar = 4 cigarettes). There were no significant differences in mean age, mean education, mean self-rated health, or mean packyears between zygosity groups.

### Measures

**Olfactory measures.**—Twins participating in SATSA were mailed a series of questionnaires in 1990 assessing health, personality, and lifestyle variables, including smoking behavior. At that time, twins received a Swedish version of the *National Geographic* Smell Survey (Wysocki & Gilbert, 1989). In the Swedish version, a translation of the questions was attached to the original *National Geographic* scratch-and-sniff forms. The Smell Survey was mailed to 606 individuals, and a total of 532 (88%) completed surveys were returned. Of the 606 surveys sent out, 454 (75%) were returned from pairs in which both twins participated. The survey included a set of six microencapsulated odorants chosen to represent a range of pleasantness, familiarity, and food relatedness. Two odorants were food related: isoamyl

acetate, a banana- or pearlike fruity odor, and eugenol, a major component of clove oil. A pleasant, nonfood aroma was provided by synthetic rose. A mixture of mercaptans (sulfurous compounds added to natural gas as a warning odor) provided an unpleasant, nonfood odor. The two final odors were musk related. Androstenone is a volatile steroid metabolite produced by many mammals; it can smell of either musk or urine. Galaxolide is a synthetic musk widely used in commercial perfumes.

Respondents were asked to scratch and sniff a panel containing each odorant and answer several questions, including "Did you smell something (yes or no)?" "Did it smell good or bad?" "How intense is this odor?" The questions concerning perceived pleasantness and perceived intensity were answered on a 5-point scale ranging from good to bad and from weak to strong, respectively. Respondents were also asked to identify the odorant by responding to the question "Which word best describes this odor?" Response options were *floral, musk, urine, foul, ink, spice, wood, fruit, burnt, sweet, and other* (if other, what?). The descriptors were chosen to provide generic-level, nonoverlapping designations of odor quality (Russell and colleagues, 1993; Wysocki & Gilbert, 1989). Odor identification was scored by using the standard answers identified by Wysocki and Gilbert (1989). If respondents provided a veridical label for the odorant, their responses were counted as correct. Also, if a participant emitted a near-miss label such as banana candy for amyl acetate, it was coded as correct. If respondents detected an odorant but proved unable to identify it, then their identification responses were scored as incorrect. Data for each question were summarized across odorants to obtain four measures: number of odorants detected (odor detection), number of odorants correctly identified (odor identification), mean perceived pleasantness, and mean perceived intensity.

**Cognitive measures.**—The SATSA cognitive test battery includes 11 cognitive measures drawn from various sources and chosen to assess four areas of cognitive ability (Pedersen et al., 1992). Verbal ability is tapped by tests of Information, Synonyms, and Analogies. Figure Logic, Block Design, and Card Rotations assess spatial abilities. Memory tests include Digit Span, Thurstone's Picture Memory, and Names and Faces. Finally, perceptual speed is measured by Digit Symbol and Figure Identification. Reliabilities for these tests range from .82 to .96. A measure of general cognitive ability was also created by obtaining individuals' scores on the first principal component of all the measures (as in Pedersen et al., 1992). All measures loaded higher than .50 on the first principal component, which accounted for 48% of the total variance.

### Statistical Method

The basic assumptions underlying the twin design are that (a) the shared environmental factors that produce similarities among twin pairs are the same for the MZ and DZ twin pairs, (b) there is no assortative mating on the traits of interest, and (c) there are no nonadditive genetic effects. Previous research with SATSA data have indicated that these assumptions are not violated in that sample (Pedersen

Table 1. Demographic Characteristics of the Sample

Characteristic	MZA		DZA		MZT		DZT	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
No. Pairs	31		72		55		69	
% Female	54.8		68.0		52.7		51.4	
Age	67.8	8.5	65.3	8.0	66.0	7.7	67.3	9.3
Education	1.41	0.7	1.48	0.8	1.58	0.9	1.64	0.9
Self-rated health	1.37	.55	1.39	.54	1.39	.51	1.38	.53
Packyears	9.71	13.8	8.15	15.7	9.34	14.7	7.58	13.5
No. odorants detected	5.32	0.8	5.33	1.1	5.26	1.0	5.40	0.8
No. correctly identified	2.37	1.1	2.63	1.1	2.41	1.0	2.45	1.1
Perceived pleasantness	2.50	0.4	2.47	0.5	2.51	0.6	2.40	0.5
Perceived intensity	3.11	0.6	3.13	0.7	3.17	0.6	3.05	0.7

Notes: MZA = monozygotic twins reared apart, DZA = dizygotic twins reared apart, MZT = MZ twins reared together, DZT = DZ twins reared together. Education was rated on a scale ranging from 1 (elementary school) to 4 (university or higher). Self-rated health was rated on a scale ranging from 1 (good) to 3 (bad). Perceived pleasantness ranged from 1 (good) to 5 (bad). Perceived intensity ranged from 1 (weak) to 5 (strong).

et al., 1992). When these assumptions are met, the total variance in a trait is typically divided into three components: genetic effects, shared environmental effects, and nonshared environmental effects. Shared environmental factors make family members more similar to each other, whereas nonshared environmental factors make family members less similar to each other. When the sample includes twins reared together and twins reared apart, however, the rearing environment can be modeled more precisely. We can differentiate between rearing environmental effects and the effects of environmental factors that happen to be correlated for twins regardless of their rearing status. In the current analyses, then, the total variance was divided into components explained by four separate influences: additive genetic effects ( $V_a$ ), correlated environmental effects ( $V_c$ ), shared rearing environmental effects ( $V_s$ ), and nonshared environmental effects including error ( $V_{ns}$ ). The phenotypic covariance between twins, assuming the four components of variance are uncorrelated, can be expressed as in the following equations for monozygotic twins reared together (MZT), monozygotic twin reared apart (MZA), dizygotic twins reared together (DZT), and dizygotic twin reared apart (DZA):

$$\begin{aligned} \text{covMZT} &= V_a + V_c + V_s \\ \text{covMZA} &= V_a + V_c \\ \text{covDZT} &= 1/2V_a + V_c + V_s \\ \text{covDZA} &= 1/2V_a + V_c, \end{aligned}$$

where covMZT represents the covariance between MZT twins. MZ twins share all their genetic material; thus, they have all of their genetic variance in common. DZ twins share, on average, one half of their segregating genes so that they have only half of their genetic variance in common. Correlated environmental effects add to the similarity of all twin pairs regardless of rearing status or zygosity. Twins reared in the same household will have in common all of the rearing environmental variance, whereas twins reared apart share no rearing environmental variance. The covariance between the nonshared environmental factors for any two individuals is, by definition, zero, thus the  $V_{ns}$  term is not included in the covariance equations.

By fitting structural models to the observed MZA, MZT, DZA, and DZT covariance matrices, we can estimate the proportion of total phenotypic variance accounted for by the variance in genetic factors (i.e., heritability), shared environment factors, correlated environment factors, and nonshared environment factors, respectively. Covariance matrices were subjected to multivariate model fitting procedures, using LISREL 8 (Jöreskog & Sörbom, 1993). Tests of subsets of the structural model were conducted to determine whether the fit of the model to the data was significantly reduced when one or more of the paths was removed from the model (Neale, Heath, Hewitt, Eaves, & Fulker, 1989). Significant reduction in model fit is indicated by a significant change in chi-square value.

To investigate the relationship between olfactory functioning and cognitive abilities, a standard Cholesky bivariate model (Neale & Cardon, 1992) was implemented. As shown in Figure 1, the model includes genetic, correlated environmental, shared rearing environmental, and non-

shared environmental influences on cognitive ability and separate genetic and environmental influences specific to olfactory functioning. The diagonal paths from the genetic and environmental influences for cognitive ability to olfactory functioning generate the Cholesky decomposition of the correlation between olfactory functioning and cognitive functioning. Paths from the latent age variable to both cognitive and olfactory functioning allow for the estimation of age variance in both traits. In total, the model permits the estimation of age, genetic, and environmental components of the correlation between cognitive ability and olfactory functioning.

## RESULTS

### Descriptive Statistics

Mean performance on the four measures of olfactory functioning is presented in Table 1. There were no significant differences in the measures between zygosity groups. The mean number of odorants detected by respondents was 5.33 ( $SD = 0.95$ ). Respondents correctly identified an average of 2.49 ( $SD = 1.11$ ) of the odorants. In their analysis of the 1.2 million responses to the *National Geographic* Smell Survey, Wysocki and Gilbert (1989) reported that respondents between the ages of 40 and 80 correctly identified between 2 and 3 odorants. Perceived pleasantness in the SATSA sample averaged 2.46 ( $SD = 0.51$ ). Mean perceived intensity was 3.11 ( $SD = 0.66$ ). In the *National Geographic* sample, mean perceived intensity ranged from 3.2 to 3.8 for adults aged 40 to 80 (Wysocki & Gilbert, 1989). Perceived intensity is an idiosyncratic measure. Minor differences between the *National Geographic* sample and the SATSA sample may result from cultural differences (e.g., Barber, 1997), variations in the actual strength of the odorants due to aging of the test forms, or random error.

All variables were corrected for the effect of sex and smoking history by regressing the variables on sex and packyears and then using the residual score for subsequent analyses. In their analysis of these data, Larsson and associates (2000) found no reliable influence of sex on the olfac-

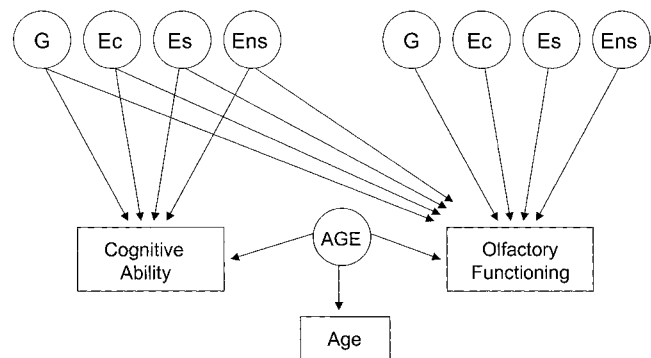


Figure 1. Cholesky bivariate path diagram. The model includes genetic (G), correlated environmental (Ec), shared rearing environmental (Es), and nonshared environmental (Ens) influences on cognitive ability and olfactory functioning. Paths from the latent age variable (AGE) to both cognitive ability and olfactory functioning allow for the estimation of age variance in both traits.

tory measures, although gender, favoring women, proved to be marginally influential for odor identification. In the calculation of phenotypic and intraclass correlations, variables were corrected for the effects of age, as well. Age was incorporated in the quantitative genetic model; therefore, for the genetic analyses, variables were corrected for sex and packyears only. Two types of quantitative genetic analyses were conducted: univariate analysis of olfactory functioning and bivariate analysis of the relationship between olfactory functioning and cognitive abilities.

**Univariate Analysis**

The first step in the univariate genetic analysis was to examine the intraclass correlations, which are presented in Table 2. If the MZ twin correlation is greater than the DZ twin correlation, then genetic effects are indicated. If the DZ correlation is greater than half the MZ correlation, then correlated environmental effects are indicated. If correlations for twins reared together are greater than correlations for twins reared apart, then rearing environmental effects are indicated. Examination of the correlations presented in Table 2 indicated some evidence for genetic effects on all four measures of olfactory functioning. In each case, the MZ correlation was greater than the DZ correlation. Only three of the correlations were significantly greater than zero, however, and the difference between MZ and DZ correlations did not attain significance. The pattern of correlations provided little evidence of rearing environment or correlated environment effects.

Patterns evident in the intraclass correlations were further examined through quantitative genetic analysis of the covariance matrices, and the results are presented in Figure 2. The total variance in each measure of olfactory functioning was divided into variance explained by age, genetic factors, shared rearing environmental factors, and nonshared environmental factors. Correlated environmental effects did not contribute to the variance in any of the measures of olfactory functioning. Age accounted for only 1% of the variance in odor identification and perceived pleasantness. Age explained 2% of the variance in perceived intensity. The influence of genetic factors was modest for all four measures of olfactory functioning, ranging from 14% for odor detection to 29% for odor identification.

After correcting for age variance, the heritabilities for the four measures of olfactory functioning were .14 for odor detection, .29 for odor identification, .17 for perceived pleasantness, and .25 for perceived intensity. Dropping the genetic parameter from the quantitative genetic model and

Table 2. Twin Intraclass Correlations

Variable	MZA	DZA	MZT	DZT
No. odorants detected	.15	-.13	.05	.00
No. correctly identified	.27	.15	.28*	.15
Mean pleasantness	.11	.00	.35**	.22
Mean intensity	.18	.02	.26*	-.03

Notes: Variables were corrected for age, sex, and packyears. MZA = monozygotic twins reared apart, DZA = dizygotic twins reared apart, MZT = MZ twins reared together, DZT = DZ twins reared together.

\**p* < .05; \*\**p* < .01.

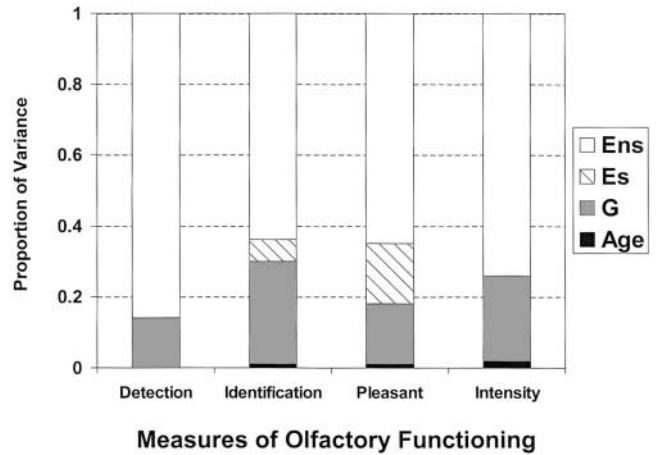


Figure 2. Results of univariate analysis. Total variance in odor detection, odor identification, perceived pleasantness, and perceived intensity has been divided into age, genetic (G), shared rearing environment (Es), and nonshared environment (Ens) components.

assessing the change in model fit tested the significance of the heritability estimates. Results indicated significant heritability for odor identification,  $\Delta\chi^2(1) = 4.45, p < .05$ , and a marginally significant heritability for perceived intensity,  $\Delta\chi^2(1) = 2.97, p < .10$ . The heritability of odor detection and perceived pleasantness failed to attain significance.

**Bivariate Analysis**

We began the bivariate analysis by examining the phenotypic correlations between the four measures of olfactory functioning and the 12 cognitive measures included in SATSA, presented in Table 3. Both olfactory functioning and cognitive measures were corrected for age, sex, and packyears. Of the 10 correlations that attained significance at the .05 level, 8 involved odor identification. For the most part, odor identification correlated with those cognitive

Table 3. Phenotypic Correlations Between the Cognitive Variables and the Measures of Olfactory Functioning

Cognitive Measures	Olfactory Functioning			
	Number Detected	Number Identified	Mean Pleasantness	Mean Intensity
Information	-.02	.20**	-.04	-.06
Synonyms	-.11*	.16**	-.08	-.02
Analogies	-.06	.15**	-.08	-.00
Figure Logic	-.01	.08	-.04	-.06
Block Design	-.06	.14*	.00	-.03
Card Rotations	-.08	.05	.00	-.06
Digit Span	-.00	.14*	.06	.03
Thurstone's Picture Memory	-.05	.16**	-.06	.02
Names & Faces	-.02	.08	-.04	-.07
Digit Symbol	-.10	.18**	.01	-.04
Figure Identification	-.06	.08	-.13**	.01
General cognitive ability	-.06	.18**	-.07	-.05
Verbal factor	-.07	.21**	-.10*	-.03

Note: Variables were corrected for age, sex, and packyears. \**p* < .05; \*\**p* < .01.

measures having a strong verbal component: Information, Synonyms, Analogies, and Thurstone's Picture Memory. Using principal-components analysis, these four measures were combined into a verbal factor. The cognitive measures were corrected for age and packyears before being entered into the principal-components analysis. The analysis resulted in a single factor that explained 62% of the total variance. Factor loadings for the four cognitive measures were .82 for Information, .89 for Synonyms, .76 for Analogies, and .64 for Thurstone's Picture Memory. The correlations between the verbal factor and the four measures of olfactory functioning are also presented in Table 3. As expected, the verbal factor was strongly correlated with odor identification. In addition, there was a modest correlation between the verbal factor and perceived pleasantness.

The next step was to examine the cross-twin, cross-trait correlations between odor identification and the relevant cognitive measures. A cross-twin, cross-trait correlation is the correlation of Trait 1 (odor identification) in Twin A with Trait 2 (cognitive ability) in Twin B. The same logic used in the examination of univariate intraclass twin correlations was applied to the examination of the bivariate cross-twin, cross-trait correlations presented in Table 4. For example, if the MZ cross-twin correlation is greater than the DZ cross-twin correlation, then there is evidence for genetic mediation of the correlation between the two traits. The pattern of cross-twin correlations for Synonyms, Analogies, the verbal factor, and to some extent general cognitive ability suggest a genetic contribution to the phenotypic correlation. The pattern of correlations found for the other cognitive measures was unclear.

The quantitative genetic model presented in Figure 1 was fit to the bivariate covariance matrices, and the results are presented in Figure 3. The correlations between odor identification and the relevant cognitive measures were divided into contributions by age, genetic factors, shared rearing environmental factors, and nonshared environmental factors. The univariate analysis provided no evidence for an influ-

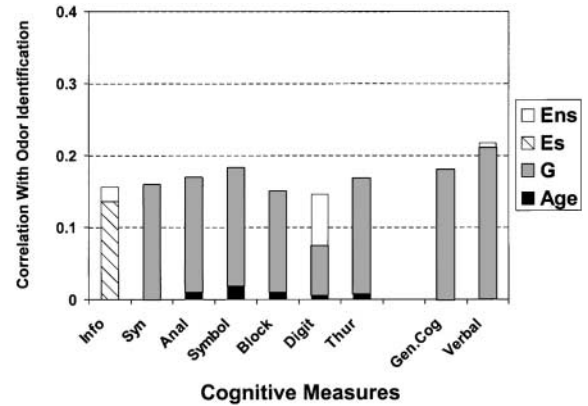


Figure 3. Results of bivariate analysis. Indicates contribution of age, genes (G), shared rearing environment (Es), and nonshared environment (Ens) to the correlations between odor detection and the cognitive variables: Information (Info), Synonyms (Syn), Analogies (Anal), Digit Symbol (Symbol), Block Design (Block), Digit Span (Digit), Thurstone's Picture Memory (Thur), general cognitive ability (Gen.Cog), and the Verbal factor (Verbal).

ence of correlated environment on odor identification; therefore, the correlated environmental component could not logically contribute to the correlation between odor identification and the cognitive measures. As a consequence, the diagonal path from the correlated environmental component for cognition to olfactory functioning (see Figure 1) was not included in the model. Results indicated that age made a minimal contribution to the correlation for only five of the variables: Analogies, Digit Symbol, Block Design, Digit Span, and Thurstone's Picture Memory. The correlations between odor identification and all but two of the cognitive measures arose primarily from genetic factors. The two exceptions were Information and Digit Span. The correlation between odor identification and Information resulted entirely from environmental factors, and the correlation between odor identification and Digit Span resulted from both genetic and environmental factors.

The correlations between odor identification and the two summary cognitive measures, general cognitive ability and the verbal factor, were primarily genetically mediated. Furthermore, in the bivariate path model including either general cognitive ability or the verbal factor, all of the genetic variance on odor identification came through the cognitive measure. In other words, there was no genetic variance for odor identification that was independent of genetic variance for the cognitive measures.

**DISCUSSION**

The goals of the present investigation were a univariate genetic analysis of olfactory functioning and a bivariate genetic analysis of the relationship between olfactory and cognitive functioning. The univariate analysis indicated at most moderate heritability for odor identification (.29) and perceived intensity (.25). Similarly, the twin correlations reported by Segal and colleagues (1995) suggested a heritability of approximately .30 for odor identification. The mean age of the twins in their sample was 26, 40 years younger

Table 4. Correlations Between Number of Odor Identification and Cognitive Measures: Phenotypic and Cross-Twin, Cross-Trait Correlations

Variable	Phenotypic Correlation	Cross-Twin, Cross-Trait Correlations			
		MZA	DZA	MZT	DZT
Information	.20**	.06	.11	.28	.04
Synonyms	.16**	.24	.08	.22	-.02
Analogies	.15**	.15	.01	.16	-.09
Digit Symbol	.18**	.13	.17	.18	-.06
Block Design	.14*	.10	.11	.03	-.03
Digit Span	.14*	.01	.15	-.02	-.06
Thurstone's Picture Memory	.16**	-.08	.12	.17	.14
General cognitive ability	.18**	.22	.20	.18	.00
Verbal factor	.21**	.22	.12	.25	.05

Notes: Variables were corrected for age, sex, and packyears. MZA = monozygotic twins reared apart, DZA = dizygotic twins reared apart, MZT = MZ twins reared together, DZT = DZ twins reared together.

\*p < .05; \*\*p < .01.

than the mean age of the present sample. It appears that there is little change in the heritability of odor identification throughout the adult lifespan; however, more data are needed to verify this conclusion. Longitudinal twin data on olfactory functioning would provide the most accurate investigation of possible age trends in genetic influences on olfactory functioning. In the absence of longitudinal data, twin data on odor identification in middle adulthood would allow us to test the hypothesis that heritability of odor identification is stable across several age cohorts in adulthood.

Heritability estimates for odor detection and perceived pleasantness, in contrast to those for odor identification, failed to attain significance in the present study. Measures of perceived pleasantness attempt to assess the idiosyncratic hedonic experience of olfactory functioning. It is not surprising, then, that most of the variance in perceived pleasantness can be attributed to nonshared environmental influences. The absence of significant genetic variance for odor detection is more difficult to interpret. The evidence for genetic and environmental influences on odor detection from previous studies was inconsistent across odorants. In the present investigation, odor detection performance was summed across six odorants commonly used in investigations of olfactory functioning. However, participants detected on average five of the six odorants. Consequently, the total variance in odor detection performance may have been restricted, diminishing our power to detect significant genetic variance. A more powerful assessment of odor detection would involve administration of increasing concentrations of the test odorants. Segal and colleagues (1995) used this method to assess detection of a single odorant and found no difference in MZ and DZ correlations. Replication of their study, incorporating detection of several odorants, might provide sufficient power to detect reliable genetic influences on odor detection.

The majority of the variance in olfactory functioning in the second half of the lifespan was explained by environmental factors, predominantly nonshared environmental factors. Although the data were corrected for the effects of smoking—one possible nonshared environmental influence on olfactory functioning—many other potential environmental factors have been proposed. Diseases such as central nervous system disorders, diabetes, stroke, and epilepsy may affect olfactory functioning (Murphy, 1999; Savic, Bookheimer, Fried, & Engel, 1997; Settle, 1986). In their analysis of data from SATSA, Larsson and associates (2000) found that central nervous system disorders were reliably related to impairments in odor detection, and epilepsy was associated with impaired odor identification. Lifestyle factors may also be a source of nonshared environmental influences. Corwin, Loury, and Gilbert (1995) reported that olfactory functioning was significantly affected by occupational experience. Factory workers demonstrated significantly impaired odor detection and lower self-ratings of olfactory ability as compared with office workers and those in other occupations.

Investigation of the relationship between cognitive abilities and olfactory functioning indicated strong positive correlations between measures of verbal ability and odor identification (Larsson et al., 2000). The specificity of this

relationship was indicated by the absence of significant correlations for other measures of cognitive abilities (spatial abilities, short-term memory) and other measures of olfactory functioning (odor detection, perceived pleasantness, and perceived intensity). A significant correlation between Digit Symbol and odor identification was also found. Although the relationship between perceptual speed and odor identification may not be readily apparent, research has indicated that the olfactory system is extremely slow relative to other sensory modalities (Herz & Engen, 1996; Laing & MacLeod, 1992). Thus, faster perceptual speed may result in better performance on measures of olfactory functioning. Alternatively, perceptual speed may influence olfactory functioning indirectly, through verbal ability. Evidence suggests that perceptual speed mediates much of the age-related variance in cognitive functioning (Salthouse, 1993, 1994). Consequently, the correlation between Digit Symbol and odor identification may reflect the underlying relationships between perceptual speed and verbal ability and between verbal ability and olfactory functioning.

Bivariate quantitative genetic analysis indicated that the relationship between odor identification and cognitive ability was primarily genetically mediated. Indeed, all of the genetic influences on odor identification could be attributed to genetic influences on verbal ability. The strong genetic mediation of the correlation between odor identification and verbal ability provides additional support for the hypothesis that odor identification and verbal ability in general tap the same cognitive domain (Larsson, 1997). The hypothesis is further supported by the finding of Larsson and associates (2000) that verbal ability remained a significant predictor for odor identification performance after statistical control of the effects of chronological age, sex, education, and global cognitive functioning. Results of the regression analysis (Larsson et al., 2000) and the quantitative genetic analysis reported here indicate the pivotal role played by verbal ability in successful odor identification.

In addition, the results of the present analyses provide some insight into the nature of age differences in olfactory functioning. Odor identification reflects the combination of the bottom-up process of sensory functioning and the top-down process of cognitive abilities (Richardson & Zucco, 1989). Univariate and bivariate quantitative genetic analyses reported here suggest the possibility that genetic influences on odor identification result from genetic effects on the top-down, or cognitive, component of the process. In contrast, environmental influences may act on the bottom-up, or sensory, component of the process. Therefore, declines in sensory functioning, per se, likely result from the accumulated effects of nonshared environmental influences, such as health or lifestyle variables. Declines in the cognitive component of performance on some olfactory measures may reflect genetically influenced cognitive decline. Mean declines in cognitive ability can result from genetic factors, even if (as our data suggest) the heritability of odor identification remains stable. The genetic influence is on the rate of change. Analyses of longitudinal twin data from SATSA, for example, indicated a significant genetic influence on the rate of decline in performance on measures of verbal ability (Reynolds, Gatz, & Pedersen, 1998). Further research will

be required to verify the differing impact of genetic and environmental influences on the components of olfactory functioning. In addition, it will be valuable to determine how olfactory functioning at one point in time is related to cognitive decline and the extent to which genes mediate that association.

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