Can Comparison of MZ- and DZ-Twin Concordance Rates be Used Invariably to Estimate Heritability?

Peter V. Tishler[1,2] and Vincent J. Carey[2]

[1] *Genetics Division, Department of Medicine, Brigham and Women's Hospital, Harvard Medical School, Boston, Massachusetts United States of America*

[2] *Channing Laboratory, Department of Medicine, Brigham and Women's Hospital, Harvard Medical School, Boston, Massachusetts, United States of America*

Proponents of the validity of the classical MZ-DZ twin comparison model for calculating heritability claim that the environments influencing MZ and DZ twin individuals are essentially identical. This 'equal environments assumption' may or may not be universally true when applied to the analysis of subjective traits. We examined the validity of this assumption as applied to the propensity for smoking cigarettes, reasoning that equality of environments should lead to equal smoking prevalences in MZ and DZ twin individuals. We identified 8 twin populations with data on smoking. We compiled odds ratios (ORs) for ever smoking in MZ and DZ twin individuals in these 8 studies and overall, using a fixed-effects meta-analytic method based on the Mantel-Haenszel procedure. The prevalence of smoking was less in MZ twin individuals than in DZ twin individuals in 7 of 8 studies. The overall OR was 0.86 (95% confidence interval 0.84, 0.89). ORs were virtually unchanged when the analyses were stratified for gender and age, and no differences were found in relation to the location of the study, the date of the study or the birth years of the cohorts. For cigarette smoking, the environments of MZ and DZ twins may not be co-equal. For subjective traits, heritability estimates may be influenced by these unequal environmental factors that differentially affect their development and characteristics in MZ and DZ twins.

A classical approach to determining whether phenomena have a hereditary basis is the comparison of concordance rates in identical (MZ) twins with those in fraternal or dizygotic (DZ) twins. On this basis, heredity has long been known to be operative in the determination of many characteristics, such as body mass index (Fabsitz et al., 1994), blood pressure (Pickering, 1968, pp. 236–273), pulmonary function (Redline et al., 1987), and many sequelae of alcoholism (Hrubec & Omenn, 1981). This model has also been applied to subjective phenomena, such as behavioral or personality traits or even the propensity to smoke cigarettes (Carmelli et al., 1992). George Engel (1975, 1987), Seymour Kety (1959) and others have illustrated and emphasized that bonding between MZ twins is extremely intense, and is much more profound than that in DZ twins or in singleton siblings. This suggests that the cultural/environmental factors that are common to or communicated between MZ co-twins might be quantitatively different from those between DZ twins, and that the augmented concordance frequently seen in behavioral traits in MZ twins versus DZ twins may be a reflection in some part of these different cultural/environmental influences. To the extent that this is true, it will confound any quantitative attempt to impute heredity or calculate heritability on the basis of MZ-DZ twin comparisons. One of us (PVT) offered this argument at the International Congress on Twin Studies in July, 2004. One rejoinder, defending the use of twin comparisons of subjective traits, was that the prevalence of smoking among individual MZ twins is no different from that in individual DZ twins. If so, this suggests that the impetus for smoking in each and every twin individual is independent of the intensity of the intratwin pair interaction. We have been unable to find published data on smoking prevalences in individual twins to substantiate this assertion. Thus, the present study addresses the prevalence of cigarette smoking among MZ and DZ twin individuals as a means of gauging the importance of shared environment in twin comparisons.

Materials and Methods

Information on cigarette smoking was drawn from previously published studies (identified by computerized literature searches) of populations of MZ and

Received 10 May, 2007; accepted 31 July, 2007.

Address for correspondence: Peter V. Tishler, M. D., Channing Laboratory, 181 Longwood Avenue, Boston, Massachusetts 02115, United States of America. E-mail: peter.tishler@channing.harvard.edu

Table 1

Characteristics of the Twin Samples Providing Smoking Data

Twin registry	Year smoking Data compiled	Ages (yr)	Sex	No. individual twins MZ	DZ	Information source
Greater Boston	1981	24–61	M/F	272	176	Tishler, 2005, (unpublished data)
US WWII vets	1968	41–51	M	4610	4940	Carmelli et al., 1992
US Vietnam vets	1987	30-49	M	5074	4158	Henderson et al., 1990; True et al., 1997; Goldberg 2005
Finland	1975	18–75 +	M/F	6724	14,375	Kaprio et al., 1978
St Thomas Hospital, UK	2004	16–86	M/F	2543	2809	Andrew et al., 2001; Hunkin & Spector, 2005
Australia	1980	18–45	M/F	2828	1740	Madden et al., 2004; Hannah et al., 1985
Denmark (old)	~1957	47–87	M/F	686	1102	Raaschou-Nielsen, 1960
Sweden (new)	1973	15–47	M/F	9940	15,528	Medlund et al., 1977
Virginia	1996	20–58	M	1526	1108	Kendler et al., 2000; Schmitt et al., 2005
Totals				34,203	45,936	

Note: For sex, M = male, F = female. Overall, the study included 80,139 twin subjects — 46,240 males and 33,899 females.

like-sexed DZ twins. An exception was the information from the Greater Boston Twin Registry, with which one of us (PVT) has been involved. These data were augmented by personal inquiries of the authors, when necessary. These studies all included populations of at least 150 MZ and DZ twin individuals of known smoking status (ever vs. never smoking), a definition of ever smoking; and, when possible, the smoking status of twin individuals stratified by age and gender. Nine twin populations in which data on smoking in individual twins were available are listed in Table 1, which also includes basic information from which the analytic covariates were derived. Appropriate smoking information was not available from at least one other study in the literature.

The index of cigarette smoking in each population was ever smoking. Prevalences of never smoking and ever smoking (computed by subtracting the number of never smokers from the total number of subjects) were derived according to definitions of smoking stipulated in each population study. These definitions, which were quite variable, are listed in Table 2. The classification of twins as MZ and like-sexed DZ twins from these individual studies was also accepted.

We compared the marginal probabilities of smoking in twins from each of the eight twin populations. The proportion of individuals reporting ever smoking was stratified by study and by MZ/DZ status, and the odds ratio comparing MZ to DZ was computed for each study. These odds ratios were combined in a fixed-effects meta-analytic framework, based on the Mantel-Haenszel procedure (Breslow & Day, 1980). The heterogeneity of the odds ratios across the studies was tested using the procedure of Woolf (1955). The software employed for these analyses was the rmeta

Table 2

Definitions of Never Smoking in Study Populations

Twin registry/study	Definition of nonsmoker (reference)
Greater Boston	< 4 pack years (Tishler, 2005, unpublished data)
US WWII Vets	'… subjects who reported that they had smoked fewer than 100 cigarettes in their lives and were not current cigar or pipe smokers' (Carmelli et al.,1992)
US Vietnam Veterans	Never smoked more than 100 cigarettes in his lifetime (True et al.,1997)
Finland	Never smoked more than 5 to 10 packs of cigarettes in whole life (Kaprio et al.,1978)
St Thomas Hospital, UK	Negative answer to "Have you ever smoked a whole cigarette?" (Hunkin & Spector, 2005)
Australia	Answer to "Have you EVER been a smoker?" (If so) "Were you ever a regular smoker?" (Madden et al., 2004)
Denmark, old	'… such persons, as have denied smoking on questionnaire without further comment' (Raaschou-Nielsen, 1960)
Sweden, new	'No' answer to "In your entire life have you smoked more than 5 to 10 packs of cigarettes?" or to "Have you ever smoked cigarettes regularly, that is, daily or almost daily?" (Medlund et al., 1977)
Virginia	'Yes' answer to "Have you ever smoked or used tobacco regularly for at least a month?" (Schmitt et al., 2005)

package, distributed at the Comprehensive R Archive Network (cran.r-project.org).

Results

The prevalence of cigarette smoking among individuals in MZ twinships was lower than that in individuals in DZ twinships in all but one of the eight studies (Table 3). Individual MZ twins smoked between 3% (World War II US Veterans) and 34% (Greater Boston twins) less than individual DZ twins. In the Danish twin registry, the frequency of smoking in MZ twins exceeded that in DZ twins by 3.7% (59.8% vs. 56.1%). These data are represented in the meta analysis of Figure 1. The overall Mantel-Haenszel Odds Ratio (OR) is 0.86, with a 95% confidence interval (CI) of 0.84 and 0.89. For this analysis, the χ^2 for heterogeneity was 29.4 (P = .0003).

We used a similar statistical approach to examine the influence of covariates. For gender, results remained virtually the same for males (OR = 0.86, CI 0.82, 0.89; heterogeneity test not significant) and females (OR = 0.87, CI 0.83, 0.91; heterogeneity test χ^2 = 15.9, P = .007) when analyzed separately (Figure 2). Stratifying by age also appeared to have little influence on the differential smoking prevalence of MZ versus DZ twins (Table 4). We found no differences in ORs as a function of location of the study, the date the data were compiled, or the birth years of the nine cohorts.

Discussion

We have examined the frequency of cigarette smoking in individuals in MZ and DZ twinships in eight twin populations. We found a lower prevalence of smoking in MZ twin individuals than in DZ twin individuals in seven of these populations and in a combined meta analysis (Figure 1). These findings are not explained or modified by the obvious covariates gender, age, year of birth, geographic location, or date of data acquisition. If each twin functioned totally independently within his/her environment, one might expect that the overall frequency of smoking in MZ and DZ twin populations would be similar. Such a similarity can be anticipated to be independent of the differential rates of concordance for smoking that have been established for MZ versus DZ twin *pairs*.

The writings of George L. Engel, long a professor of Psychiatry and Medicine at the University of Rochester School of Medicine (USA), are perhaps the most vivid description and analysis of the intensity of the relationship between MZ twins. Writing of his own relationship with his MZ twin brother, both in life and after his brother's premature death, Engel emphasizes the fusion of identities and boundaries (said another way, the diffuseness of ego boundaries between MZ twins), complementarity of being (extreme physical similarity), thought and action (e.g., enjoying a private language), and the narcissistic gains of twinship (Engel, 1975). Whereas the relationship between MZ twins has been described as 'the closest tie between two individuals' (Burlingham, 1945), that between DZ twins has been characterized as similar to that of singleton siblings (Penninkilampi-Kerola et al., 2005). Moreover, the intrauterine environment may also differ significantly between DZ and MZ twins (Phillips, 1993; Loos et al., 2001). These observations suggest that studies comparing concordance rates of MZ twins with DZ twins should factor in these dissimilar cultural/environmental factors to minimize any nongenetic augmentation of MZ concordance. Nonetheless, researchers have concluded that the equal environments assumption — the underlying premise that 'environmentally caused similarity is roughly the same for both types of twins reared in the same family' — is valid (Tandon & McGuffin, 2002; Plomin et al., 2001). The arguments asserting the validity of the equal environments assumption, including the results of studies of traits in MZ twins reared apart, of the similarities of MZ twins who were mislabeled (as DZ) and treated as such by their parents, and of the comparative similarities of MZ twins treated more individually versus those not treated so individually, are summarized by Plomin et al. (2001). Others have documented specific examples of dissimilar environments, but found no effects of this differential background on certain aspects of behavior (Morris-Yates et al., 1990).

Recent studies from Finland appear to challenge the equal environments assumption, however. Penninkilampi-Kerola et al. (2005a, 2005b) have studied the concordance of a number of traits in a cohort of teenaged MZ and DZ twins. A measure of co-twin dependence ('a strong attachment between twins') was established by asking each twin, at age 16, whether he/she was 'dependent' on his/her co-twin. The answer, yes or no, permitted the creation of a dependent group and an independent group of twins, in which both members of the pair answered the question similarly. Co-twin dependence varied considerably by twin type and gender, ranging from about 30% and 37% for MZ boys and girls, respectively, to about

Table 3

Overall Prevalence of Cigarette Smoking in MZ and DZ Twins

Twin Study	% Ever Smoking Individual Twins		D(MZ–DZ), %
	MZ	DZ	
Greater Boston	41.9	63.1	–21.2
US WWII Vets	71.2	73.3	–2.1
US Vietnam Vets	67.6	71.7	–4.0
Finnish	45.1	48.9	–3.8
St Thomas, UK	56.7	62.6	–5.9
Australian	44.2	46.7	–2.5
Old Danish	59.8	56.1	3.7
New Swedish	52.7	56.4	–3.7
Virginia	48.4	54.9	–6.5

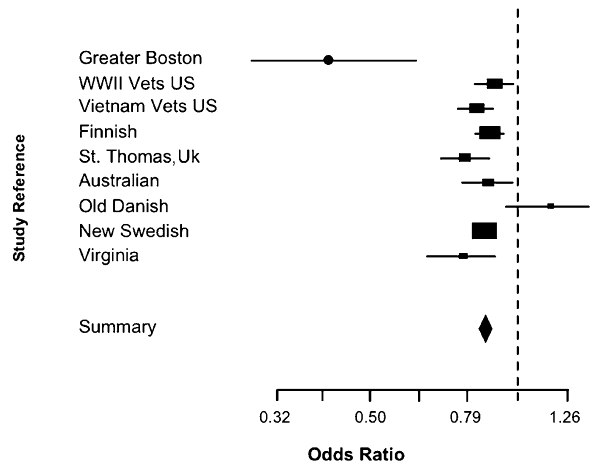

Figure 1

Odds ratios for cigarette smoking in all MZ twins vs. all DZ twins in the nine individual studies and the combined statistic. The overall Mantel-Haenszel odds ratio = 0.86 (95% CI 0.84, 0.89).

15% and 26% for same-sexed DZ twin boys and girls, respectively. This dependency was especially associated with having the co-twin as a best friend, and also with the proportion of leisure time spent together, the mothers' educational level and the fathers' socio-economic status. For the use of alcohol in adolescence and early adulthood, most correlations of the co-twin dependent group exceeded those of the co-twin independent group, suggesting a greater similarity of alcohol-related behavior of co-twin dependent twins. Co-twin dependent twins also differed from the co-twin independent twins in the

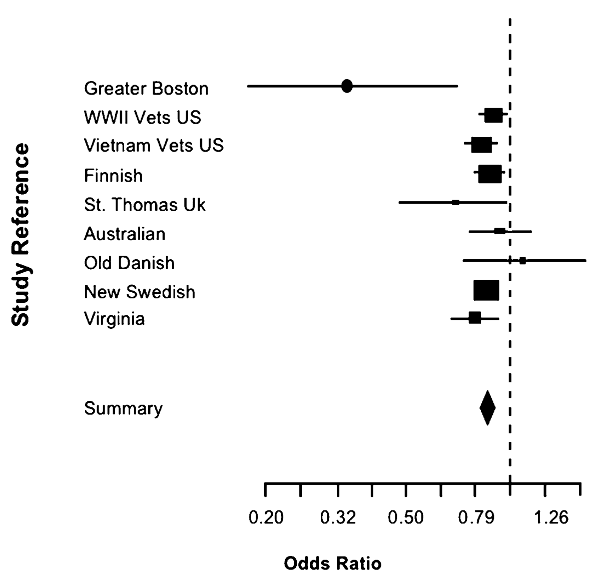

Figure 2

Odds ratios for cigarette smoking in MZ twins vs. DZ twins stratified by gender. For males, the Mantel-Haenszel odds ratio = 0.86(95% CI 0.82, 0.89); for females, this odds ratio = 0.87 (95% CI 0.83, 0.91).

frequency of reporting of 'somatic and psycho-emotional symptoms' (Penninkilampi-Kerola et al., 2004). These researchers, while reviewing in detail the uniqueness and intensity of prior studies focusing on the relationship of MZ co-twins, emphasize that 'we can also expect that co-twin dependent twins might be more similar to each other because they evidently share their social environment to a greater extent than independent twins. This has implications for studies of heritability in twins because a fundamental assumption of classical twin studies is that MZ and DZ twins represent the same base population and that MZ and DZ twins are equally correlated in their exposure to environmental influences relevant to the trait under study.' (Penninkilampi-Kerola et al., 2005a). Their studies would call into question the equal environments assumption. The disparity that we have demonstrated in rates of smoking between MZ and DZ twins further suggests that differences in concordance between MZ versus DZ twins may not be ascribable to genetic factors related to the variable under analysis, and that, at least for some subjective or cultural factors, common environment may confound the estimation of heritability. Alternatively, one can ascribe some proportion of the dependence of MZ co-twins to inheritance, but this would equally distort estimates of heritability of other factors, particularly those related to behavior, when derived from MZ-DZ twin comparisons. We suggest, as have others, that the classical twin study can serve as 'the nucleus of a systematic genetic approach to the study of human behavior,' (Hewitt, 1989), but the accuracy of such a study will depend in large part on recognizing and minimizing the effects of differential environments.

Kendler and co-workers found a similar phenomenon in their study of the illicit use of psychoactive substances: the rates of abuse of six different types of substance were higher in MZ than in DZ twins (Kendler et al., 2000). Applying models to their data that were designed to detect and correct for the effects of the equal environment assumption, they found only a small effect of correlated environment in the six parameters of drug abuse to which these models were applied. This did lead to a considerable reduction in the estimate of heritability in one of the parameters of illicit drug use, however. One could conclude, as the authors did, that 'it is unlikely that the overall results of this investigation were substantially biased by violations of the equal environment assumption'. However, one can take the opposite view: the marked overestimate in heritability in one of six cases suggests that this phenomenon may be more pervasive than currently recognized. Kendler and Gardner (1998) describe similar phenomena in a study of psychiatric disorders and substance abuse in adult twins. The extent of social interaction was significantly greater in MZ than in DZ twin pairs, but this was not predictive of twin resemblance for a number of behavioral phenomena (e.g., anxiety disorder, nicotine dependence). On the other

Table 4

Prevalence of Cigarette Smoking in MZ versus DZ Twin Individuals Stratified by Age*

Age, Yr	No subjects (studies)	Ever smokers, %		Odds ratio	95% CI
		DZ Twins	Δ(MZ – DZ)		
16-25	22,796 (4)	54.7	–5.3	0.81	0.76, 0.85
26-35	17,797 (6)	51.5	–1.3	0.95	0.89, 1.01
36-44	28,955 (7)	61.1	–4.5	0.83	0.79, 0.88
45-59	5948 (4)	37.5	–4.8	0.81	0.72, 0.92
60+	3173 (2)	37.7	–1.1	0.95	0.81, 1.12

Note: *Includes data from all registries except Denmark and Virginia, which could not be subdivided by age.

hand, co-socialization significantly predicted twin resemblance for smoking initiation and perhaps for bulimia. For the smoking initiation, factoring in the differential environmental effect reduced the heritability modestly (from 83% to 73%).

The present study is limited by data acquired by other researchers and the biases that were built into these studies. It was also limited by our inability to obtain relevant information on cigarette smoking in other large studies of twin populations, suggesting a further bias in our analyses. As corroborated by the significant tests of the odds ratios for heterogeneity, the populations that were exploited herein are clearly heterogeneous at least in size, gender, age, birth year, dates of study, and country of origin — the variables whose influence we assessed. This is both a weakness, limiting the reliability of meta analysis, but also a strength, serving in many cases to demonstrate that differences in smoking between MZ and DZ twins were not influenced or explained by these covariates. In our statistical analyses, we are not able to adequately factor in the lack of statistical independence of twins, since we do not have access to primary data. We believe, however, that correcting for any intratwinship correlation is unlikely to eliminate the effects we have reported.

In summary, we have found a significant difference in the prevalence of smoking in MZ versus DZ twins. This difference cannot be explained by such covariates as gender, age, country of origin of the study, dates during which the study was conducted, or the birth years of the cohort. This finding raises the possibility that using the MZ–DZ comparison model for determining heritability of subjective traits may have limitations. While the difference in the overall smoking rates in MZ and DZ twins is not great, it is nonetheless persistent. One might anticipate variable, and sometimes larger, MZ–DZ differences, and thus differently inflated heritability estimates, for other subjective traits that have been studied by this classical twin method. This will not be obtained for all subjective traits, and the effect, when present, will be variable. We suggest, as have others (Rose et al., 1990), that measurements of the effects of MZ- and DZ-specific environment be incorporated into all twin studies, and that these data be used to minimize the confounding effects of environment on heritability estimates.

References

Andrew, T., Hart, D. J., Snieder, H., de Lange, M., Spector, T. D., & MacGregor, A. J. (2001). Are twins and singletons comparable? A study of disease-related and lifestyle characteristics in adult women. *Twin Research*, 4, 464–477.

Breslow, N. E., & Day, N. E. (1980). *Statistical methods in cancer research. Vol. 1. The analysis of case-control studies*. Lyon: International Agency for Research on Cancer.

Burlingham, D. (1945). The fantasy of having a twin. *Psychoanalytic Study of the Child, 1,* 205–210.

Carmelli, D., Swan, G. E., Robinette, D., & Fabsitz, R. (1992). Genetic influence on smoking: A study of male twins. *The New England Journal of Medicine*, 327, 829–833.

Engel, G.L. (1975). The death of a twin: Mourning and anniversary reactions. Fragments of 10 years of self-analysis. *The International Journal of Psycho-Analysis*, 56, 23–40.

Engel, G. L. (1987). Where you *think* you stand determines what you *think* you see. *Pharos*, *50,* 21–24.

Fabsitz, R. R., Sholinsky, P., & Carmelli, D. (1994). Genetic influences on adult weight gain and maximum body mass index in male twins. *American Journal of Epidemiology*, 140, 711–720.

Goldberg, J. H. (2005). Personal communication.

Hannah, M. C., Hopper, J. L., & Mathews, J. D. (1985). Twin concordance for a binary trait. II. Nested analysis of ever-smoking and ex-smoking traits and unnested analysis of a 'committed-smoking' trait. *American Journal of Human Genetics*, *37,* 153–165.

Henderson, W. G., Eisen, S., Goldberg, J., True, W. R., Barnes, J. E., & Vitek, M. E. (1990). The Vietnam era twin registry: A resource for medical research. *Public Health Reports*, *105,* 368–373.

Hewitt, J. K. (1989). Of biases and more in the study of twins reared together: A reply to Grayson. *Behavior Genetics*, *19,* 605–608.

https://doi.org/10.1375/twin.10.5.712 Published online by Cambridge University Press

Hrubec, Z., & Omenn G. S. (1981). Evidence of genetic predisposition to alcoholic cirrhosis and psychosis: Twin concordances for alcoholism and its biological end points by zygosity among male veterans. *Alcoholism: Clinical and Experimental Research*, *5*, 207–215.

Hunkin, J., & Spector, T. D. (2005). Personal communication.

Kaprio, J., Sarna, S., Koskenvuo, M., & Rantasalo, I. (1978). *The Finnish Twin Registry: Baseline characteristics. Section II. History of symptoms and illnesses, use of drugs, physical characteristics, smoking, alcohol and physical activity*. Helsinki: University of Helsinki.

Kendler, K. S., & Gardner, C. O., Jr. (1998). Twin studies of adult psychiatric and substance dependence disorders: Are they biased by differences in the environmental experiences of monozygotic and dizygotic twins in childhood and adolescence? *Psychological Medicine, 28,* 625–633.

Kendler K. S., Karkowski L. M., Neale, M. C., & Prescott, C. A. (2000). Illicit psychoactive substance use, heavy use, abuse, and dependence in a US population-based sample of male twins. *Archives of General Psychiatry*, *57,* 261–269.

Kety, S. S. (1959). Biochemical theories of schizophrenia. *Science*, *129,* 1590–1596.

Loos, R. J. F., Beunen, G., Fagard, R., Derom, C., Vlietinck, R., & Phillips, D. I. W. (2001). Twin studies and estimates of heritability. *Lancet*, *357,* 1445.

Madden, P. A. F., Pedersen, N. L., Kaprio, J., Koskenvuo, M. J., & Martin, N. G. (2004). The epidemiology and genetics of smoking initiation and persistence: Crosscultural comparisons of twin study results. *Twin Research*, *7,* 82–97.

Medlund, P., Cederlof, R., Floderus-Myrhed, B., Friberg, L., & Sorensen, S. (1977). A new Swedish twin registry. *Acta Medica Scandinavica*, *600*.

Morris-Yates, A., Andrews, G., Howie, P., & Henderson, S. (1990). Twins: A test of the equal environments assumption. *Acta Psychiatrica Scandinavica*, 81, 322–326.

Penninkilampi-Kerola, V., Kaprio, J., Moilanen, I., Ebeling, H., & Rose, R. J. (2004). Co-twin dependence and twins' psycho-emotional well-being and health from adolescence to early adulthood: A longitudinal study of development and health of five consecutive birth cohorts of Finnish twins. *Twin Research*, *7,* 371–372 (abstract).

Penninkilampi-Kerola, V., Moilanen, I., & Kaprio, J. (2005a). Co-twin dependence, social interactions, and academic achievement: A population-based study. *Journal of Social and Personal Relationships*, *22,* 519–541.

Penninkilampi-Kerola, V., Kaprio, J., Moilanen, I., & Rose, R. J. (2005b). Co-twin dependence modified heritability of abstinence and alcohol use: A population-based study of Finnish twins. *Twin Research and Human Genetics*, *8,* 232–244.

Phillips, D. I. W. (1993). Twin studies in medical research: Can they tell us whether diseases are genetically determined? *Lancet*, *341,* 1008–1009.

Pickering, G. (1968). *High blood pressure* (2nd ed.). London: J. & A. Churchill.

Plomin, R., DeFried, J. C., McClearn, G. E., & McGuffin, P. (2001). *Behavioral genetics* (4th ed., pp. 72–83). New York: Worth Publishers.

Raaschou-Nielsen, E. (1960). Smoking habits in twins. *Danish Medical Bulletin*, *7,* 82–88.

Redline, S., Tishler, P. V., Lewitter, F. I., Tager, I. B., Munoz, A., & Speizer, F. E. (1987). Assessment of genetic and nongenetic influences on pulmonary function: A twin study. *American Review of Respiratory Disease*, *135,* 217–222.

Rose, R. J., Kaprio, J., Williams, C. J., Viken, R., & Obremski, K. (1990). Social contact and sibling similarity: facts, issues, and red herrings. *Behavior Genetics*, *20,* 763–778.

Schmitt, J. E., Prescott, C. A., Gardner, C. O., Neale, M. C., & Kendler, K. S. (2005). The differential heritability of regular tobacco use based on method of administration. *Twin Research and Human Genetics*, *8,* 60–62.

Tandon, K., & McGuffin, P. (2002). The genetic basis for psychiatric illness in man. *European Journal of Neuroscience*, *16,* 403–407.

True, W. R., Heath, A. C., Scherrer, J. F., Waterman, B., Goldberg, J., Lin, N., Eisen, S. A., Lyons, M. J., & Tsuang, M. T. (1997). Genetic and environmental contributions to smoking. *Addiction*, *92,* 1277–1287.

Woolf, B. (1955). On estimating the relationship between blood group and disease. *Annals of Human Genetics*, *19,* 251–253.

https://doi.org/10.1375/twin.10.5.712 Published online by Cambridge University Press