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Genetic Factors in Physical Activity and the Equal Environment Assumption – the Swedish Young Male Twins Study

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The aims of this study were to examine the genetic contribution on physical activity (PA) within a nationwide population of young adult male twin pairs from Sweden and to investigate the equal environment assumption (EEA) in relation to PA. Information on PA was collected by questionnaires in 1998 and 2002 and the impact of genetic factors was estimated by structural equation modeling (SEM). The study included 1022 pairs of twins and the best fitting SEM-model gave a heritability of 49% (95% CI, 40–56%) for total PA and all PA dimensions showed genetic contributions between 40% and 65%. Non-shared environmental factors were also important, whereas shared environmental factors did not contribute to PA behaviors. The EEA was investigated with a linear regression model, examining if the twins contact frequency predicted within-pair differences in PA, and further by a simulation study. We found no support for violation of the EEA.

KEY WORDS: Environment; epidemiology; genetics; physical activity; twins.

INTRODUCTION

Physical activity (PA) is of key importance for energy expenditure. The increasing prevalence of overweight and obesity worldwide is explained by excess energy intake in relation to energy expenditure. However, heterogeneity in risk for developing overweight and obesity may partly be explained by genetic factors influencing the expenditure side of the energy balance equation. Studies on the role of genetic and environmental factors on PA behavior have shown genetic contributions to PA (heritability) in the range of no effect to 0.83 depending on age, gender, study design, studied PA dimension and methods used for assessing PA (Aarnio *et al.*, 1997; Beunen and Thomis, 1999; Boomsma *et al.*, 1989; Heller *et al.*, 1988; Kaprio *et al.*, 1981; Lauderdale *et al.*, 1997; Maia *et al.*, 2002; Perusse *et al.*, 1988, 1989; Simonen *et al.*, 2002, 2004). One study has identified chromosomal regions with genes that may contribute to PA level (Simonen *et al.*, 2003b) and several other studies have found associations between different genes and PA (Loos *et al.*, 2005; Simonen *et al.*, 2003a; Stefan *et al.*, 2002). Evidence for a role of genes in PA behavior has also emerged from experimental research on animals. One study showed that rats with higher percentage of type II muscle fibers in their leg muscles spontaneously ran longer and at higher velocity than rats with lower percentage type II fibers (Suwa *et al.*, 2003). Another study found that mice with reduced skeletal muscle mass and fewer type I fibers spontaneously ran shorter distance during a 6 day period compared with controls (Kamei *et al.*, 2004). Swallow *et al.* (1998) reported an average increase of 75% in activity level in mice

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after 10 generations of selection for high levels of voluntary wheel-running.

The twin study design provides a powerful tool for examining the contributions of genetic and environmental factors to behavioral traits. It has been claimed, however, that this design is flawed by higher within-pair correlations among monozygotic (MZ) than dizygotic (DZ) twins in environmental factors influencing some behavioral traits. Under such circumstances the equal environment assumption (EEA), i.e. that MZ and DZ twins experience equally correlated environments of etiological importance for the trait, might be invalid and the heritability would be overestimated (Neale and Cardon, 1992). To our knowledge, the EEA has not previously been explored for PA behavior. When testing the EEA for eating behavior, Klump *et al.* (2000) did not find support for the hypothesis that within-pair resemblance is affected by degree of physical or other similarities. Evans and Martin (2000) found evidence that strongly suggests that the classical twin design does not violate the EEA. A recent simulation study showed that stratification of twin correlations by amount of contact can yield spurious evidence of shared environmental effects in some strata and even give false indications of non-additive genetic effect or genotype–environment interaction (Eaves *et al.*, 2003). Such results might indeed be an effect of genetic factors on so-called “niche selection”, i.e. the groups or environments people choose to join and live in.

We have conducted a study on a large population-based cohort of young adult male twin pairs from Sweden. The objectives were to further explore the genetic contribution to PA and thus energy expenditure among young men and to shed light on the potential risk of violating the EEA in twin studies on PA behavior. We achieved these goals by analyzing empirical as well as simulated twin data.

MATERIAL AND METHODS

Study Population

The present study is based on the Swedish Young Male Twins Study, which started in 1998 (Rasmussen and Johansson-Kark, 2002). The cohort comprises all male twins born 1973–1979 listed in the Swedish Medical Birth Register and residing in Sweden in 1997. For the 3566 eligible twins (1783 pairs) a record-linkage was made to the Military Service Conscription Register and data on height and weight were obtained from this source. The 3566 twins were also asked to answer a mailed questionnaire in 1998. Of these, 2810 (79%) returned the questionnaire and 2726 twins had complete information on PA. Two-thousand and sixty four twins were classified as either MZ or DZ and part of a complete pair. Ten pairs were excluded due to severe handicaps or diseases and a total of 2044 twins were included in the analyses. In 2002, 3484 twins were followed up with a second questionnaire. Of these 2169 (62%) responded and 2078 had information on at least one PA dimension (please see below). One-thousand four hundred and ninety twins were classified as MZ or DZ and part of a complete pair, of whom 248 twins (124 pairs) gave discordant answers on contact frequency and were therefore excluded. Four pairs were excluded due to severe handicaps or diseases. A total of 1234 twins were included in the analyses of the survey 2002.

Zygosity

Information on zygosity was collected in both 1998 and 2002. Zygosity was determined by two widely used and validated questions on physical resemblance during childhood and difficulties teachers might have had in distinguishing between the twins (Cederlöf *et al.*, 1961; Pedersen and Lichtenstein, 2000). Pairs where both stated to be “as alike as two peas in a pod” and that teachers “always or nearly always” had problems in distinguishing them were classified as MZ. Pairs where both answered “not more alike than siblings in general” to the first question and “seldom” or “never or almost never” to the second question were classified as DZ. All remaining pairs were classified as undetermined zygosity (XZ). Ten pairs who differed in their answers in 1998 and 2002 were classified as XZ.

The 139 complete pairs who were classified as XZ were offered a DNA test to determine their zygosity. In 34 pairs one or both twins did not complete the test. The twins who consented rinsed their mouth with Scope mouthwash solution (Proctor & Gamble) and DNA was purified from buccal cells as described elsewhere (Heath *et al.*, 2001). Zygosity was determined by using 16 highly polymorphic micro-satellite markers from Weberset 6. A pair was considered MZ if concordant for all 16 markers and DZ if they differed in more than one marker. No pair differed in one marker and all the 105 pairs were classified as either MZ or DZ. Analysis software used were GeneScan version 3.5.1 and GenoTyper version 3.7 NT.

Physical Activity and Frequency of Contact within Twin Pairs

Information on PA was collected by questionnaires in 1998 and 2002. In both years the following two global questions were used: "How physically active have you been in your daily work, studies or occupation during the last 12 months?" and "How physically active have you been in your leisure time during the last 12 months?" The response alternatives were (1) sedentary work/leisure time, (2) light activity (not sweating), (3) moderate activity (sweating), and (4) vigorous activity (sweating and breathing hard). In 2002, we added a modified version of the Baecke questionnaire (Baecke *et al.*, 1982; Pols *et al.*, 1995), which covers four dimensions: (1) occupational PA, (2) leisure time PA excluding sport, (3) sport during leisure time, and (4) total PA. The scores on the dimensions are on a continuous scale and were regarded as normally distributed. The Baecke questionnaire has been validated against energy expenditure assessed by the double-labeled water method (Livingstone and Black, 2003) and found valid and reliable (Pols *et al.*, 1995; Philippaerts *et al.*, 1999). Occupational PA and leisure time PA including sport assessed by the two questions described above correlated strongly (in 2002) with the corresponding dimensions of the Baecke questionnaire, occupational PA 0.85 (95% CI, 0.83–0.86) and sport during leisure time 0.82 (95% CI, 0.81–0.84).

The twins contact frequency in 2002 was assessed with the question: "How often do you usually get together with or speak to your twin brother?" with nine response alternatives from every day to once a year. Twin pairs where both answered every day and/or several times a week were classified as having frequent contact and pairs where both answered once a week or less often were classified as having infrequent contact.

Statistical Analysis

Structural equation modeling (SEM) (Neale and Cardon, 1992) was used in univariate heritability analyses of the different PA dimensions. The total phenotypic variation can be decomposed into the four latent (unmeasured) variance components: additive genetic effects (A), non-additive (dominance) genetic effects (D), environmental effects *shared* by individuals (C) and environmental effects *not shared* by individuals (E). Heritability in the broad sense is defined as the proportion of the total phenotypic variation that is due to the genetic components A and/or D (Evans *et al.*, 2002). Under this genetic model, SEM can be used to estimate the variance components from which heritability estimates can be derived.

The response alternatives of the two questions used for assessment of PA in both 1998 and 2002 were, as previously described, ordinal with four categories and therefore so-called liability-threshold models were used. These models only assume that the observed outcomes for the two twins, which are measured on ordinal scales, reflect an underlying bivariate normally distributed liability of the trait. To estimate variance components and confidence intervals, SEM was fitted directly to the contingency tables by maximum likelihood with the software Mx (Neale *et al.*, 2002; Sham, 1998). The scores on the four dimensions of the Baecke questionnaire were regarded as normally distributed and modeled on a continuous scale. Data preparation for contingency tables and other descriptive statistics were done in SAS (SAS Institute, 1999). The SEM-models ADE, ACE, AE, CE and E were fitted and then compared by Akaike's Information Criteria (AIC) (Akaike, 1987) and also tested with a chi-squared goodness-of-fit index. The model with the smallest AIC is considered to represent the best compromise between goodness-of-fit and parsimony. Model fit was also assessed by the root means square error of approximation (RMSEA) (Neale *et al.*, 2002). Models with RMSEA values below 0.1 are considered having good fit and those with RMSEA below 0.05 very good fit.

To investigate the EEA, the absolute within-pair score differences on the Baecke questionnaire were assessed with a linear regression model, adjusted for zygozity, and comparisons were made between groups with frequent and infrequent contact.

The simulation study was carried out under the conditions used by Eaves *et al.* (2003). In these simulation analyses no shared environmental effects were allowed, which means that differences in estimates between MZ and DZ twins could not be due to different within-pair correlations in shared environmental factors. Niche selection was, however, allowed. It is assumed that the measured trait, here PA, contributes to a latent trait that, together with other genetic and environmental factors, has impact on niche selection. Examples of possible niches are peer groups, sport and educational activities.

Assessment of Potential Selection Bias

The 1234 twins (617 twin pairs) included in the analyses of the survey 2002 were compared to the 2250 twins not included (due to non-participation in the survey 2002, missing data or being part of an incomplete pair) for differences in age, body mass index (BMI, kg/m^2) from conscription examination at age 18 and educational level from the 1998 survey. BMI was available for 91% of the twins included and for 90% of the twins not included in the analyses and educational level for 92% and 69%, respectively. Comparisons of mean differences for BMI, date of birth and proportion of high vs. low education, as well as the comparisons between MZ and DZ twins, were carried out with *t*-tests derived using generalized mixed models adjusting for within-pair correlations and heterogeneity between zygosity groups. Distributions of PA between MZ and DZ twins were compared with the Wilcoxon's rank-sum test.

RESULTS

The twins included in the analyses were on average 25 days younger than those not included ($p = 0.33$) and they did not differ with respect to mean BMI at conscription examination at age 18 years (Diff = 0.14, $p = 0.26$). There was, however, a larger proportion of high-educated subjects (more than upper secondary school) among the included twins than among the not included twins (41.1% vs. 35.1%, $p = 0.008$).

Mean of BMI was slightly lower among the MZ (23.6 kg/m^2) than among the DZ twins (23.8 kg/m^2) ($p = 0.45$). According to WHO criteria for overweight (BMI $\geqslant$ 25 kg/m^2) and obesity (BMI $\geqslant$ 30 kg/m^2), 26.5% of the DZ twins and 23.1% of the MZ twins were overweight ($p = 0.23$), while 2.4% of DZ twins and 2.9% of MZ twins were obese ($p = 0.66$). Of the MZ twins, 10.2% reported their leisure time PA during the previous 12 months as sedentary, 27.5% as light, 35.0% as moderate and 27.3% as vigorous. The corresponding figures for the DZ twins were 11.2%, 24.3%, 39.8%, and 24.6% ($p = 0.80$). Of the MZ twins, 39.6% reported their occupational PA during the previous 12 months as sedentary, 25.8% as light, 27.4% as moderate and 7.2% as vigorous. The corresponding figures for the DZ twins were 36.9%, 27.5%, 26.3%, and 9.3% ($p = 0.28$).

The within-pair correlations for the different PA dimensions were about twice as high for MZ compared with DZ twins, indicating presence of genetic effects on PA behavior (Table I).

The best fitting SEM model was the AE-model, which had the lowest AIC-value for all PA dimensions (Table II). This conclusion was also supported by χ^2-tests. Both AIC and χ^2-tests clearly showed that non-genetic models (E and CE) fit significantly much worse than models including genetic components and also that the more complex models (ACE and ADE) did not significantly improve model fit. In the ACE-models for all PA dimensions, the shared environment (C) was estimated to be zero or very close to zero. All AE-models had RMSEA values of 0.031 or less suggesting that the AE-models fit very well to observed data. We therefore present estimates from the AE-models, which suggests that PA is influenced by additive genetic (A) and non-shared environmental factors (E). In 1998, the heritability estimates for occupational PA and leisure time PA including sport were 0.60 (95% CI, 0.53–0.65) and 0.65 (95% CI, 0.59–0.70), respectively. The corresponding heritabil-

Table I. Within-Pair Correlations of the Different Physical Activity Dimensions

Measure of physical activity and year of survey	Dimension of physical activity	Correlations (95% CI) DZ	Correlations (95% CI) MZ
Global questions 1998	Leisure time PA incl. sport[a]	0.34 (0.25–0.44)	0.64 (0.59–0.70)
	Occupational PA[a]	0.34 (0.24–0.44)	0.59 (0.52–0.65)
Global questions 2002	Leisure time PA incl. sport[a]	0.33 (0.20–0.46)	0.54 (0.45–0.63)
	Occupational PA[a]	0.27 (0.13–0.41)	0.53 (0.44–0.62)
The Baecke questionnaire 2002	Total PA[b]	0.19 (0.04–0.33)	0.46 (0.37–0.54)
	Occupational PA[b]	0.23 (0.09–0.36)	0.58 (0.51–0.65)
	Leisure time PA excl. sport[b]	0.18 (0.05–0.30)	0.39 (0.30–0.48)
	Sport during leisure time[b]	0.32 (0.20–0.43)	0.55 (0.48–0.62)

[a] Polychoric correlations.

[b] Pearson correlations.

Table II. Model Fit Statistics of the Different SEM-Models of Physical Activity Dimensions. The Best Fitting Model was the AE-Model

Measure of physical activity and year of survey	Dimension of physical activity	Statistic	ADE[b]	ACE[c]	AE	CE[d]	E[e]
Global questions 1998	Leisure time PA incl. sport	AIC	1.07	0.90	**−0.93**	26.81	259.77
		χ^2 (*p*-value[a])	45.07 (1)	44.90 (0.68)	45.07	72.81 (<0.001)	307.77 (<0.001)
	Occupational PA	AIC	−11.98	−12.70	**−13.98**	2.28	195.68
		χ^2 (*p*-value[a])	32.02 (1)	31.30 (0.40)	32.02	48.28 (<0.001)	243.68 (<0.001)
Global questions 2002	Leisure time PA incl. sport	AIC	−13.08	−13.70	**−15.08**	−8.68	92.22
		χ^2 (*p*-value[a])	30.92 (1)	30.30 (0.43)	30.92	37.32 (0.008)	140.22 (<0.001)
	Occupational PA	AIC	−16.84	−16.84	**−18.84**	−8.27	74.84
		χ^2 (*p*-value[a])	27.16 (1)	27.16 (1)	27.16	37.73 (0.001)	122.84 (<0.001)
The Baecke questionnaire 2002	Total PA	AIC	−5.85	−5.48	**−7.48**	6.15	83.58
		χ^2 (*p*-value[a])	0.15 (0.54)	0.52 (1)	0.52	14.15 (<0.001)	93.58 (<0.001)
	Occupational PA	AIC	−5.97	−5.37	**−7.37**	17.60	131.52
		χ^2 (*p*-value[a])	0.03 (0.43)	0.63 (1)	0.63	25.60 (<0.001)	141.52 (<0.001)
	Leisure time PA excl. sport	AIC	−5.59	−5.19	**−7.19**	3.41	58.45
		χ^2 (*p*-value[a])	0.41 (0.53)	0.81 (1)	0.81	11.41 (0.001)	68.45 (<0.001)
	Sport during leisure time	AIC	−5.66	−5.99	**−7.66**	6.74	141.65
		χ^2 (*p*-value[a])	0.34 (1)	0.008 (0.56)	0.34	14.74 (<0.001)	151.65 (<0.001)

[a] *p*-values from likelihood ratio test with 1 df for testing difference in chi-square between nested models.
[b] ADE-AE.
[c] ACE-AE.
[d] ACE-CE.
[e] AE-E.

ity estimates for 2002 were somewhat lower and are shown in Table III along with estimates stratified by contact frequency between the twin brothers. When the same analyses were conducted on twins who had complete data on PA in both surveys (514 pairs), similar results were obtained. The estimate for occupational PA in 1998 was a little higher (0.64 (95% CI, 0.56–0.72) whereas the estimate for leisure time PA including sport in 1998 and the estimates for 2002 did not change. These results indicate that heritability was lower in 2002 than in 1998. High contact frequency (more than once a week) was reported by 80–81% of the MZ pairs and 54–56% of the DZ pairs, depending on the PA dimension studied. The heritability estimates in 2002 were consistently higher among twin pairs with frequent contact, suggesting a potential violation of the EEA.

Table IV shows the results from the SEM analyses of the four dimensions of the Baecke questionnaire. The highest heritability estimate was obtained for occupational PA and the lowest for leisure time PA excluding sport. In all PA dimensions, the estimate was higher among the pairs with frequent contact.

To examine whether the EEA might be invalid for PA in this twin population, the means of the absolute within-pair score differences on the Baecke

Table III. Heritability (a^2) of Occupational Physical Activity and Leisure Time Physical Activity Including Sport Measured by Global Questions in 2002 and Assessed by Structural Equation Modeling, Stratified by Contact Frequency. 359 MZ and 232 DZ Twin Pairs

Dimension of physical activity	Contact frequency	Additive genetic factors a^2 (95% CI)	Non-shared environmental factors e^2 (95% CI)
Leisure time PA including sport	All	0.55 (0.46–0.63)	0.45 (0.37–0.54)
	Frequent[a]	0.58 (0.49–0.67)	0.42 (0.33–0.51)
	Infrequent[b]	0.43 (0.21–0.61)	0.57 (0.39–0.79)
Occupational PA	All	0.54 (0.44–0.62)	0.46 (0.38–0.55)
	Frequent[a]	0.57 (0.48–0.66)	0.43 (0.34–0.53)
	Infrequent[b]	0.36 (0.12–0.57)	0.64 (0.43–0.88)

[a] 291 MZ and 126 DZ pairs.
[b] 68 MZ and 106 DZ.

questionnaire, adjusted for zygosity, were compared between twins with frequent and infrequent contact. The differences were −0.024 for occupational PA ($p = 0.47$), 0.034 for leisure time PA excluding sport ($p = 0.13$), 0.008 for sport during leisure time ($p = 0.84$), and 0.012 for total PA ($p = 0.87$). Results from the same analyses performed on MZ and DZ twins separately did not find any significant differences. Nor was there a significant interaction between contact frequency and zygosity for any PA dimension. Thus, these results do not indicate a violation of the EEA.

To further investigate whether the EEA might be invalid for PA as assessed in the present study, simulation analyses were conducted according to Eaves *et al.* (2003). Data were simulated with additive (A) and non-shared environmental (E) factors for 20,000 MZ and 20,000 DZ twin pairs. The within-pair correlations for PA were set to 0.6 for MZ and 0.3 for DZ twins, which suggests a heritability of 0.6. The simulations were performed using the contact frequencies from our Swedish data with slight rounding. Eighty percent of the MZ twin brothers and 55% of the DZ brothers had frequent contact with each other in the simulations conducted under the presumption of no violation of the EEA. The simulations included a niche correlation component as shown in Table V. The results show clear-cut differences in the heritability estimates between twin pairs with frequent and infrequent contact, solely due to niche selection. It is also noted that the differences in heritability between pairs with frequent and infrequent contact increase by increasing amount of niche correlation (Table V).

DISCUSSION

Strengths and Limitations

The present Swedish study has strengths and limitations. Its population-based nature and the rather large sample size are strengths. The study population consists of young men only, in a narrow age-range, making questions about possible effects of age variations less relevant. This also implies that no inferences can be made about children, women or older men. The non-participation rate was high, but comparisons between twins with complete or partial non-response to the questionnaire in 2002 and those actually included in the study showed only small differences. The study participants had somewhat higher educational level than non-participants, but the groups did not differ with respect to mean age in 2002 or BMI at age 18. It thus seems plausible that the non-response only impacted on our results by decreasing statistical power. Another strength of this study is the fact that PA in 2002 was assessed by the Baecke questionnaire, which has been shown to have high validity when compared with energy expenditure assessed by double-labeled water (Philippaerts *et al.*, 1999). As described above, the global questions on occupational PA and leisure time PA including sport correlated strongly with the corresponding dimensions of the Baecke questionnaire (in 2002), which suggests that they are reasonably good measures of PA. The available crude measure of contact frequency between twins and their co-twins may not have fully disclosed to what extent the MZ and DZ twin pairs experienced equally correlated environments of importance for PA.

Table IV. Heritability (a^2) of the Physical Activity Dimensions Measured by the Baecke Questionnaire in 2002 and Assessed by Structural Equation Modeling, Stratified by Contact Frequency

Dimension of physical activity	Contact frequency	MZ pairs *N*	DZ pairs *N*	Additive genetic factors a^2 (95% CI)	Non-shared environmental factors e^2 (95% CI)
Total PA	All	305	170	0.49 (0.40–0.56)	0.51 (0.44–0.60)
	Frequent	243	94	0.53 (0.44–0.62)	0.47 (0.38–0.56)
	Infrequent	62	76	0.30 (0.09–0.48)	0.70 (0.52–0.91)
Occupational PA	All	323	195	0.57 (0.50–0.64)	0.43 (0.36–0.50)
	Frequent	257	106	0.59 (0.51–0.66)	0.41 (0.34–0.49)
	Infrequent	66	89	0.46 (0.27–0.62)	0.54 (0.38–0.73)
Leisure time PA excluding sport	All	357	227	0.40 (0.31–0.48)	0.60 (0.52–0.69)
	Frequent	289	127	0.42 (0.32–0.50)	0.58 (0.50–0.68)
	Infrequent	68	100	0.33 (0.13–0.50)	0.67 (0.50–0.87)
Sport during leisure time	All	356	222	0.56 (0.49–0.62)	0.44 (0.38–0.51)
	Frequent	288	123	0.59 (0.52–0.66)	0.41 (0.34–0.48)
	Infrequent	68	99	0.38 (0.18–0.54)	0.79 (0.77–0.82)

Table V. Simulation Analyses of Heritability (a^2) of Physical Activity, Including 20,000 MZ and 20,000 DZ Twin Pairs. Within-Pair Correlations of Physical Activity were Set to 0.6 for MZ and 0.3 for DZ and Within-Pair Contact Frequencies were Set to Values Observed in the Empirical Twin Study[a,b]

Niche correlation	Contact frequency[a,b]	Additive genetic factors a^2 (95% CI)	Non-shared environmental factors e^2 (95% CI)
MZ = 0.30[c]	All	0.60 (0.59–0.60)	0.40 (0.40–0.41)
DZ = 0.15[c]	Frequent[a]	0.66 (0.65–0.66)	0.34 (0.34–0.35)
	Infrequent[b]	0.37 (0.34–0.39)	0.63 (0.61–0.66)
MZ = 0.50[c]	All	0.60 (0.59–0.61)	0.40 (0.39–0.41)
DZ = 0.25[c]	Frequent[a]	0.68 (0.67–0.68)	0.32 (0.32–0.33)
	Infrequent[b]	0.31 (0.29–0.34)	0.69 (0.66–0.71)
MZ = 0.70	All	0.60 (0.59–0.60)	0.40 (0.40–0.41)
DZ = 0.35	Frequent[a]	0.73 (0.72–0.73)	0.27 (0.27–0.28)
	Infrequent[b]	0.21 (0.18–0.23)	0.79 (0.77–0.82)

[a] Frequent contact: MZ 80% (16,000 pairs) and DZ 55% (11,000 pairs).

[b] Infrequent contact: MZ 20% (4,000 pairs) and DZ 45% (9000 pairs).

[c] Niche correlations according to Eaves *et al.* (2003).

Resemblance in Physical Activity and Previous Research

There are considerable inconsistencies in the literature regarding the magnitude of familial resemblance in PA (Beunen and Thomis, 1999; Simonen *et al.*, 2002). Estimates of intra-class correlations and heritability depend on type of family relations and the studied PA dimension. Heritability estimates range from none or weak (Perusse *et al.*, 1989) to moderate (Lauderdale *et al.*, 1997) and even high (Boomsma *et al.*, 1989). Most, but not all studies, have found no shared environmental effects on PA behavior (Simonen *et al.*, 2002).

In the present study we found moderate to high genetic contributions to PA, heritability in the range of 0.40–0.65, depending on PA dimension. These estimates are in agreement with several other twin studies (Beunen and Thomis, 1999; Kaprio *et al.*, 1981; Maia *et al.*, 2002; Simonen *et al.*, 2004). We did not find any effect of shared environment in the studied PA dimensions. Only additive genetic and non-shared environmental factors seem to be of importance for the variation in PA in this young adult male population. The same pattern was seen in a Portuguese study of adolescent and young adult twins. In that study a high genetic effect was found on leisure time PA excluding sport (0.68) and sport during leisure time (0.63) among the male participants and no or weak effect of shared environment (Maia *et al.*, 2002). These researchers also used the Baecke questionnaire for assessment of PA.

Since our study includes men only, it is not possible to draw inferences about genetic contributions on PA in women, as mentioned above. Previous studies have found smaller genetic influences on sports participation and daily PA for women than men and influences of shared family environment among women (Beunen and Thomis, 1999; Maia *et al.*, 2002). The mechanisms through which the genetic influences are expressed are unknown, but might be different for men and women.

In a study of 3344 middle-aged twin pairs from the USA, Lauderdale *et al.* (1997) reported heritability estimates in the range of 0.48–0.53 for specific intense activities such as running and racquet sports. Further, these authors suggested that genetic factors might have stronger influence on regular participation in specific intense physical activities than on moderate activities such as walking for recreation or exercise. Consistent with Lauderdale *et al.* (1997), our study showed lower heritability estimates for leisure time PA excluding sport than for sport during leisure time (0.40 and 0.56, respectively).

Changes of Heritability by Age

In our study the heritability estimate of occupational PA was higher in 1998 (0.64) than in 2002 (0.54). Similarly, the heritability estimate of leisure time PA including sport was higher in 1998 (0.65) than in 2002 (0.55). The influence of unshared environmental factors on PA may thus increase with age when young adult individuals complete their education, marry and settle down. These observations are in line with another population-based twin study, which showed lower heritability for PA among Finnish men 30–39 years of age (0.52) than among those 18–29 years of age (0.64) (Kaprio *et al.*, 1981).

The Equal Environment Assumption and Beyond

The EEA is a critical assumption in the classic twin study design and has been examined and found valid for behavioral traits such as eating behavior, emotional problems and psychiatric disorders (Cronk *et al.*, 2002; Kendler and Gardner, 1998; Klump *et al.*, 2000). The present Swedish study is, to our knowledge, the first to explore whether the EEA is valid in relation to PA. Our empirical results, with no shared environmental effects but heterogeneity of additive genetic components, i.e. heritability, over strata of contact frequency, may incautiously be interpreted as indicating a violation of the EEA. However, as shown in our simulation study, similar patterns of heterogeneity may arise due to genetic factors impacting on niche selection, e.g. the type of peer groups young people choose to join and spend their time with (Eaves *et al.*, 2003). The simulation analyses thus provide an interpretation of our empirical results without violation of the EEA. This is further supported by our analyses of the within-pair score differences on the Baecke questionnaire, where no differences were found between twin pairs with frequent and infrequent contact. However, we can not completely rule out a violation of the EEA since there might be other environmental factors not captured by contact frequency that make MZ twin pairs more alike. As described above we found a trend towards a greater impact of genes on PA behavior in younger ages than later in life. Also the impact of genes on niche selection may be greater in adolescence and young adulthood than in later life. The importance of genes in niche selection is supported by a study on cannabis abuse in a population of female twins, which showed that MZ twins more often than DZ twins tend to share friends and go to the same events (Kendler and Prescott, 1998). The authors concluded that MZ twins seem to prefer the same kind of social activities because they are genetically identical and that social expectations seem to play only a minor role. A study of older twins also found genetic effects on aspects of social support, e.g., support from friends (Bergeman *et al.*, 2001). In a review of peer influence on adolescent drug use, Bauman and Ennett (1996) concluded that selection of peers may contribute substantially to the association between drug use behavior of friends and that the effect of peer influence may be overestimated. However, several cross-sectional studies have reported significant associations between peer influence and PA behavior (Anderssen and Wold, 1992; Wold and Anderssen, 1992). Our simulation results and the study of Eaves *et al.* (2003) suggest that what ostensibly seems to be shared environmental influences by peers on PA might instead be consequences of genetic factors impacting on peer selection. This interpretation is further supported by a simulation study on assessment of peer selection and peer influence (Madden *et al.*, 2002). However, Horwitz *et al.* (2003) proposed that shared environmental factors play an important role and suggested that the social environment influences the degree to which genetically based qualities are selected.

CONCLUDING REMARKS

Despite growing awareness in the general public and public health recommendations about the health benefits of regular PA, sedentary life styles and physical inactivity comprise an enormous public health problem. According to the World Health Report (2002) by WHO, physical inactivity is estimated to cause 1.9 million deaths annually and is a significant contributor to the global burden of disease (World Health Organization, 2002). Our finding of a moderate to high genetic contribution to PA behaviors have potentially important implications for public health strategies aimed to increase PA in our obesogenic society. Genetic heterogeneity in PA and perhaps in genes predisposing to selection of more or less obesogenic social and physical environments (niches) may be important to consider in future public health strategies aimed at increasing PA and reducing overweight and obesity in our societies.

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