

1 Eating behaviours in healthy young adult twin pairs discordant for body mass index
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22 Running head: Eating behaviours in BMI-discordant twins

23 **1. Abstract**

24 We aimed to study which eating behavioural traits associate with body mass index
25 (BMI) among BMI-discordant twin pairs. This cross-sectional study examined self-
26 reported eating behaviours in 134 healthy young adult twin pairs (57 monozygotic
27 [MZ] and 77 same-sex dizygotic [DZ]), of whom 29 MZ and 46 DZ pairs were BMI-
28 discordant (BMI difference ≥ 3 kg/m²). In both MZ and DZ BMI-discordant pairs, the
29 heavier co-twins reported being less capable of regulating their food intake optimally
30 than their leaner co-twins, mainly due to “frequent overeating”. Furthermore, the
31 heavier co-twins reported augmented “disinhibited eating”, “binge-eating scores” and
32 “body dissatisfaction”. The twins agreed more frequently that the heavier co-twins
33 (rather than the leaner co-twins) ate more food in general, and more fatty food in
34 particular. No significant behavioural differences emerged in BMI-concordant twin
35 pairs. Overeating – measured by “frequent overeating”, “disinhibited eating”, and
36 “binge-eating score” – was the main behavioural trait associated with higher BMI,
37 independent of genotype and shared environment.

38

39 Keywords: Twins, body mass index, obesity, eating behaviour, disinhibition,
40 overeating

41 Eating behaviours involve dietary and psychological traits in regulation of food intake
42 and weight management. Eating behaviours vary strongly between individuals, and
43 are regulated by complex interactions between physiological, psychological,
44 environmental, and genetic factors (Grimm & Steinle, 2011). Obesity is considered to
45 be primarily caused by overconsumption (Swinburn, Sacks, & Ravussin, 2009), which
46 is a plausible consequence of disrupted eating behavioural traits (Bryant, King, &
47 Blundell, 2007; Bublitz, Peracchio, & Block, 2010; van Strien, Herman, & Verheijden,
48 2012). Although subjects with obesity seldom self-report higher energy intake than do
49 those at a healthy weight (Goris, Westerterp-Plantenga, & Westerterp, 2000;
50 Pietiläinen et al., 2010), obesity and increased body mass index (BMI) have, in
51 questionnaires on eating behavioural patterns, been consistently associated with
52 disinhibition of eating (Bryant et al., 2007).

53 The disinhibited eating measure encompasses social, taste, and emotional
54 triggers for overeating (Hyland, Irvine, Thacker, Dann, & Dennis, 1989). Emotional
55 eating (as a result from negative emotions) and external eating (vulnerability to
56 tempting food signals) may moderate the relationship between overeating and weight
57 increase in adults (van Strien et al., 2012). Perhaps as a consequence of weight
58 gain, individuals with obesity are often dissatisfied with their bodies (Weinberger,
59 Kersting, Riedel-Heller, & Luck-Sikorski, 2016), which in turn may be one motivation
60 to lose weight (Vartanian, Wharton, & Green, 2012). A common weight-loss approach
61 is dietary restraint; a cognitive effort to self-restrain caloric intake (Lowe, Whitlow, &
62 Bellwoar, 1991). Its relationship with BMI is complex and ambiguous. Dietary restraint
63 seems to be necessary for the treatment of obesity through energy restriction, though
64 it may increase risk for eating pathology and obesity if practiced inappropriately
65 (Schaumberg, Anderson, Anderson, Reilly, & Gorrell, 2016).

66 When investigating predictors of obesity, it is relevant to control for genetic
67 factors. Currently over 500 genetic loci related to adiposity traits have emerged
68 through genome-wide association studies (Loos, 2018), and many of these loci are
69 also associated with eating behaviours (Grimm & Steinle, 2011).

70 One can control for genetic factors through the phenotype-discordant
71 monozygotic (MZ) twin pair method (Vitaro, Brendgen, & Arseneault, 2009), a unique
72 example of a case-control study wherein participants are fully matched for genotype,
73 sex, age, and shared environmental factors, but vary in a particular variable such as
74 BMI. Any behavioural differences within MZ twin pairs are plausibly due to
75 environmental experiences and exposures that are unique to one of the twins in that
76 pair. In dizygotic (DZ) twin pairs, behavioural differences result from both
77 environmental and genetic differences, because they share approximately 50% of
78 their segregating genes.

79 Studies employing an obesity-discordant MZ twin design with twins rating their
80 eating behaviours in relation to their co-twin's (Pietiläinen et al., 2010; Rissanen et
81 al., 2002), have revealed that most twin pairs agree that the co-twins with obesity eat
82 more food overall (Pietiläinen et al., 2010; Rissanen et al., 2002), prefer fatty food
83 (Rissanen et al., 2002), and consume less healthy food (Pietiläinen et al., 2010). This
84 implies that these behaviours are associated with acquired obesity. In another study,
85 including both MZ and DZ twins, ingestion of more food in general was the strongest
86 independent correlate of intra-pair BMI differences (Bogl, Pietiläinen, Rissanen, &
87 Kaprio, 2009).

88 Overall, most studies have only investigated a limited number of eating
89 behavioural traits in relation to obesity in the same population, and therefore lack a
90 more global view on the patterns behind weight control (French, Epstein, Jeffery,

91 Blundell, & Wardle, 2012). Several studies have also been unable to control for any
92 genetic influences on the association between eating behaviours and obesity.
93 Building upon current knowledge of eating behaviours and obesity by assessing a
94 wide variety of eating behavioural traits within healthy young adult BMI-discordant MZ
95 and DZ twin pairs, we attempted to uncover which eating behavioural traits are
96 associated with BMI independent of genetic background and of shared environmental
97 factors.

98

99 **2. Materials and Methods**

100 *2.1 Participants*

101 This cross-sectional study included 134 young adult twin pairs (57 MZ and 77 same-
102 sex DZ twin pairs, aged 22 to 36), of whom 29 MZ and 46 DZ pairs were BMI-
103 discordant (BMI difference ≥ 3 kg/m²). The cut-off point for BMI-discordance was
104 defined earlier (Hakala, Rissanen, Koskenvuo, Kaprio, & Rönnemaa, 1999;
105 Rönnemaa et al., 1997). The remaining 28 MZ and 31 DZ BMI-concordant twin pairs
106 (BMI difference < 3 kg/m²) functioned as reference groups to compare eating
107 behaviours when BMI within the twin pairs was similar. Recruitment was from two
108 population-based longitudinal studies of ten complete Finnish birth cohorts from
109 1975-1979 and 1983-1987 (FinnTwin12 and FinnTwin16, n=5,417 pairs) (Kaprio,
110 2013), with data retrieved between 2003 and 2013. We took advantage of all the
111 follow-up time points after age 20 from wave 4 in FinnTwin12 (mean age 22 years)
112 and both waves 4 and 5 follow-ups in FinnTwin16 (i.e. ages 25 and 35 years) to find
113 the rare BMI-discordant MZ twins. If the twin pair had attended twice, the latter year
114 was selected. For the DZ twins, we only studied BMI-discordant pairs from the 25-
115 year follow-up of the FinnTwin 16 because at that age a sufficiently large group was

116 achieved. Additionally, a statistician created an algorithm to randomly select BMI-
117 concordant twin pairs to approximately match the number of discordant twin pairs.
118 Participants were enrolled based on their responses to questions on height and
119 weight at a young adult age, with the aim to cover the full BMI range of subjects with
120 healthy weight and with obesity, and a wide range of intra-pair BMI differences. One
121 exclusion criterion for all twins was clinical diagnosis of an eating disorder, or any
122 mental or medical disease, in order to investigate common variations in eating
123 behavioural traits, not those induced by disease or disorder. Informed consent came
124 from all individual participants included in the study. The study was approved by the
125 Ethics Committee of Helsinki University Central Hospital.

126

127 *2.2 Anthropometric measurement*

128 Height and weight were measured objectively to calculate BMI. Fat mass and body
129 fat percentage were assessed with dual energy x-ray absorptiometry (DEXA).

130 Zygosity of the twin pairs was confirmed through genotyping of multiple genetic
131 markers from large genotyping arrays with hundreds of thousands of genetic variants
132 (Illumina 670 & Illumina Human CoreExome chips). More details on anthropometric
133 assessment methods can be found in (Jukarainen et al., 2016).

134

135 *2.3 Food diary*

136 To create a basic dietary profile, the participants kept a 3-day food diary (two working
137 days and one non-working day). A registered dietician provided instructions for the
138 dietary-intake recording, using the program Diet32 (nowadays AivoDiet) to calculate
139 food consumption and energy intake (Mashie FoodTech Solutions AB, 2017); this is

140 based on 'Fineli'; the Finnish National Food Composition Database (Finnish food
141 composition database., 2009).

142

143 *2.4 Food intake regulation*

144 The twins selected one from four statements about their to ability to regulate food
145 intake (Supplementary Text S1), as in earlier studies (A. Keski-Rahkonen et al.,
146 2007; Anna Keski-Rahkonen et al., 2005; Pietiläinen et al., 2010): Shortened
147 descriptions of the answer categories were “1. Optimal eating, 2. Frequent
148 overeating, 3. Frequent restricted eating, and 4. Alternating overeating and
149 restriction”. However, due to sparse data for some uncommon behaviours, we
150 collapsed categories 2, 3, and 4 into one category for data analysis, creating a single
151 variable with two values: “non-optimal eating” versus “optimal eating”.

152

153 *2.5 Eating behaviour*

154 Four eating behaviour questionnaires were used in this study. The Three Factor
155 Eating Questionnaire (TFEQ), to investigate cognitive restraint of eating, disinhibited
156 eating, and susceptibility to hunger (Stunkard & Messick, 1985). These TFEQ
157 outcome measures were further divided into seven subscales: flexible control
158 (gradual and subtle approach of limiting food intake) and rigid control (all-or-nothing
159 approach) (Westenhoefer, 1991); habitual, emotional, and situational susceptibility to
160 disinhibition (Bond, McDowell, & Wilkinson, 2001); and internal locus for hunger
161 (regulated and interpreted internally) and external locus for hunger (triggered by
162 external cues) (Bond et al., 2001). The Dutch Eating Behaviour Questionnaire
163 (DEBQ) comprises emotional eating, external eating, and restrained eating (van
164 Strien, Frijters, Bergers, & Defares, 1986). The Binge-eating Scale (BES) assessed

165 the severity of and preoccupation with binge eating (Gormally, Black, Daston, &
166 Rardin, 1982). Three variables from the Eating Disorder Inventory-2 (EDI-2) included
167 were drive for thinness, body dissatisfaction, and bulimia (Garner, 1991).

168 The DEBQ, TFEQ, and EDI-3 (similar to EDI-2) are valid and reliable
169 measures for individuals with overweight and obesity when compared to leaner
170 controls (Bohrer, Forbush, & Hunt, 2015). BES is a valid and reliable measure for
171 both objective and subjective binge-eating severity (Timmerman, 1999).

172

173 *2.6 Co-twin comparison questionnaire*

174 Co-twins rated each other's eating behaviours in the previous 12 months through a
175 questionnaire that inquired about ten dietary intake and related behavioural aspects,
176 answering "which of you (you or your co-twin)...", for example, "...eats more?, ...eats
177 more fatty foods?, ...eats more slowly?" (Supplementary Text S2), see also (Bogl et
178 al., 2009).

179

180 *2.7 Data analysis*

181 Stata/SE 13.0 (StataCorp, College Station, TX) served for statistical analyses. Non-
182 parametric statistical tests were performed because of small sample size and non-
183 normal distribution of the majority of the data. All statistical tests we performed,
184 unless stated otherwise, within BMI-discordant and -concordant MZ and DZ twin
185 pairs separately. The cut-off point to indicate statistical significance was $p < 0.05$.
186 Since not all questionnaire data was complete, a table of the number of twin pairs
187 who completed each questionnaire is in the supplementary material (Supplementary
188 Table S1), which is available on the Cambridge Core website.

189

190 *2.7.1 Anthropometry and food diary*

191 Intra-pair differences in the anthropometric measures were examined with Wilcoxon
192 signed-rank tests, and this test also compared dietary intake and macronutrient
193 proportion in the leaner versus heavier co-twins. Anthropometry measures were
194 compared between leaner MZ and DZ co-twins, and heavier MZ and DZ co-twins
195 with Mann-Whitney U tests. Calorie intake and relative consumption of
196 macronutrients (fat, protein, carbohydrates, and alcohol) in grams per day, and in
197 percentages of energy intake, were calculated according to Fineli (the Finnish food
198 composition database. 2009). All other dietary components appeared as grams
199 consumed per day.

200

201 *2.7.2 Food intake regulation*

202 The prevalence of optimal eating and non-optimal eating between leaner and heavier
203 co-twins was examined by McNemar's test. Prevalence of optimal and non-optimal
204 eating was reported, as well as absolute prevalence differences.

205

206 *2.7.3 Eating behaviours*

207 Scores on the separate domains of the TFEQ, DEBQ, BES, and EDI-2 were adjusted
208 to a scale of 0-100 for easier interpretation and comparison (Lauzon et al., 2004),
209 which means that the lowest possible score was subtracted from the actual score and
210 divided by the possible score range, multiplied by 100 (Lauzon et al., 2004). For
211 example, suppose the total score ranges from 12 to 40. If someone scored 26, then
212 the calculation would be $(26 \text{ (actual score)} - 12 \text{ (lowest score possible)}) \div (40-12$
213 $\text{ (score range)}) \times 100 = 50$. The original cut-off points for interpretation of the BES
214 score were "severe binge-eating if BES score ≥ 27 , moderate bingeing, 18-26, and

215 no bingeing, ≤ 17 " [24]. The new scale of 0-100 gave as cut-off points "severe binge-
216 eating if BES score ≥ 59 , moderate bingeing, 38-58, and no bingeing, ≤ 37 ". The
217 other questionnaires were evaluated as higher score reflecting more extreme
218 behaviour.

219 First, survey regression analyses assessed coefficients for the association
220 between standardized behavioural traits (i.e. divided by standard deviation) and BMI
221 as a continuous variable in all twin individuals. A correction was applied for the
222 familial grouping of traits, with age and sex included as covariates. BMI, because of
223 its intuitive interpretation, was not standardized. Behaviour standardization enabled
224 equal comparison between associations with BMI.

225 Subsequently, we analyzed the differences in responses on the TFEQ, DEBQ,
226 BES, and EDI-2 questionnaires between leaner and heavier co-twins with Wilcoxon
227 signed-rank tests. We quantified the size of the significant differences with the
228 common language effect size (McGraw & Wong, 1992). This effect size identifies
229 those cases in which the heavier co-twin scores higher on a behavioural trait than
230 does the leaner co-twin as a proportion of the total twin pairs. Thus, put simply: an
231 effect size of 0.68 for emotional eating signifies that the chance is 68% that in any
232 random twin pair, the heavier co-twin experiences higher level of emotional eating.
233 Importantly, an effect size of 0.50 implies that any difference between co-twins is due
234 solely to chance. Hence, an effect size above 0.50 implies a probability superior to
235 chance that the heavier co-twin performs a behavioural trait more strongly, whereas
236 below 0.50, the heavier co-twin is less likely to do so. We calculated approximate
237 confidence intervals (CI) for effect sizes, as discussed in more detail elsewhere
238 (Altman & Bland, 2011).

239 Additionally, we created a correlation matrix of all eating behavioural traits –
240 with a correction for familial clustering – to obtain a better understanding of the
241 overlap or similarity between traits.

242

243 *2.7.4 Co-twin comparison questionnaire*

244 The co-twin comparison questionnaire we analyzed separately for MZ and DZ twins –
245 but we combined BMI-discordant and -concordant twins – in two ways: with Wilcoxon
246 signed-rank tests and multivariate regression analyses, as earlier (Bogl et al., 2009).

247 Only those twin pairs who provided internally consistent answers as to who
248 performed a particular eating behaviour more strongly we included in the Wilcoxon
249 signed-rank tests. The twin pairs were separated into Twin1 (who performed the
250 behaviour more strongly according to both co-twins of the pair), and Twin2 (who
251 performed the behaviour to a lesser extent). Wilcoxon signed-rank tests compared
252 the differences between the average BMI of Twin1 and Twin2, for all eating
253 behavioural traits, providing the mean difference in BMI (kg/m^2) for each eating
254 behavioural trait.

255 Multivariate regression analyses were performed in all twin pairs. A twin pair
256 was coded -1 if both co-twins agreed that the leaner co-twin performed the
257 behaviour, +1 if both agreed the heavier co-twin performed the behaviour, and 0 in all
258 other cases. This allowed linkage of independent eating behavioural to intra-pair
259 differences in BMI (BMI heavier co-twin - BMI leaner co-twin), while controlling for
260 age and sex.

261 **3. Results**

262 *3.1 Characteristics and dietary profile in leaner versus heavier co-twins*

263 All adiposity measures were higher in the heavier co-twins of MZ and DZ pairs
264 discordant for BMI (Table 1), as expected with this study design. The leaner co-twins
265 of the MZ twins were on average in the overweight category, and the heavier co-
266 twins in the obesity class I category. In the DZ twin pairs, the leaner co-twins on
267 average were of a healthy weight and the heavier co-twins had overweight.
268 Moreover, in the BMI-concordant twins, small intra-pair differences in adiposity were
269 evident, because of the division into leaner and heavier co-twins (Supplementary
270 Table S2). An overview of all BMI category (e.g. overweight, obesity class I)
271 comparisons in the whole cohort, and separately by zygosity and BMI-discordance is
272 available (Supplementary Table S3).

273 In BMI-discordant twin pairs, both leaner and heavier MZ co-twins had a
274 higher age, BMI, fat mass, and fat percentage than the leaner and heavier DZ co-
275 twins (Supplementary Table S4), and higher weight in leaner MZ co-twins only. Sex
276 and height followed similar patterns between MZ and DZ co-twins. No evidence was
277 present for any difference in BMI-concordant twin pairs between leaner MZ and DZ
278 co-twins or heavier MZ and DZ co-twins.

279 The food diaries did not reveal any meaningful differences in caloric intake or
280 relative intake of macronutrients between leaner and heavier co-twins in any of the
281 groups (Supplementary Table S5).

282 Table 1: Intra-pair differences in characteristics of MZ and DZ twin pairs discordant for BMI.

	BMI-discordant twin pairs							
	MZ (n=29)				DZ (n=46)			
	Leaner	Heavier	$\Delta\%$	p-value	Leaner	Heavier	$\Delta\%$	p-value
Age, y	30.1±0.9	30.0±0.9	-	-	27.4±0.3	27.5±0.3	-	-
Female/male, freq.	19/10	19/10	-	-	21/25	21/25	-	-
Height, cm	172.6±2.1	172.9±2.0	0.2	0.52	173.3±1.2	174.8±1.3	0.9	0.12
Weight, kg	76.6±3.4	94.9±3.9	23.9	<0.001	65.0±1.4	87.6±1.9	35.0	<0.001
BMI, kg/m ²	25.6±1.0	31.6±1.1	23.4	<0.001	21.5±0.4	28.7±0.6	33.5	<0.001
Fat mass, kg	25.6±2.2	39.3±2.2	53.5	<0.001	14.8±1.2	31.1±1.7	110.1	<0.001
Body fat, %	32.3±1.9	41.4±1.4	28.2	<0.001	22.3±1.6	35.2±1.6	57.8	<0.001

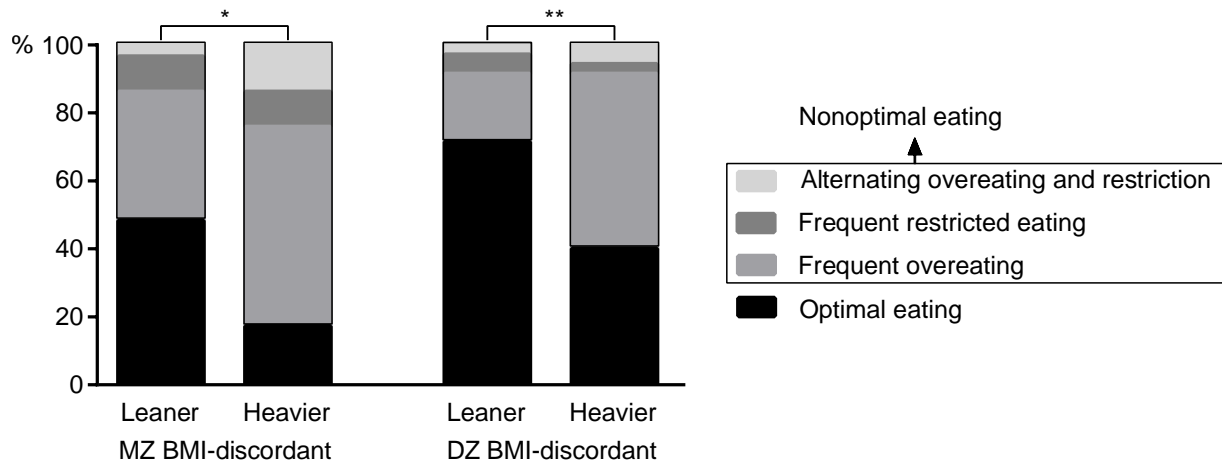
283 Values are mean±standard error. BMI=body mass index, MZ=monozygotic, n=number of pairs,
 284 DZ=dizygotic, $\Delta\%$ =difference in percentages [(heavier-leaner)/leaner×100], freq.=frequency.

285

286 3.2 Food intake regulation in leaner versus heavier co-twins

287 In MZ and DZ BMI-discordant twin pairs, McNemar’s test indicated that regarding
 288 food intake regulation, leaner and heavier co-twins differed (MZ: $\chi^2=7.36$, $p=0.01$;
 289 DZ: $\chi^2=9.31$, $p=0.003$; Figure 1). The non-optimal eating prevalence in leaner versus
 290 heavier co-twins was 52% versus 83% in MZ pairs, and 29% versus 60% in DZ pairs.
 291 Thus, in both MZ and DZ pairs, the absolute prevalence of non-optimal eating was
 292 31% higher in the heavier co-twins. Less than half of the leaner MZ (48%), but the
 293 majority of leaner DZ (71%) co-twins ate optimally. The majority of the heavier co-
 294 twins in the MZ (59%) and DZ (51%) BMI-discordant groups frequently overate. Only
 295 a few individuals in all groups frequently restricted their food intake (3–13%). In the
 296 BMI-concordant groups, leaner and heavier co-twins (58–71%) mainly ate optimally
 297 (Supplementary Figure S1), and thus did not differ in food intake regulation.

298



299

300 Figure 1: Percentages of food intake regulation categories in leaner and heavier monozygotic (MZ)
 301 and dizygotic (DZ) twins discordant for body mass index (BMI). McNemar's test * $p < 0.05$, ** $p < 0.01$.
 302

303

3.3 Eating behaviours in leaner versus heavier co-twins

304 P-values from survey regression analyses in all twin individuals demonstrated strong
 305 evidence for the presence of associations of standardized disinhibited eating,
 306 restrained eating, binge-eating score, drive for thinness, body dissatisfaction, and
 307 bulimia with BMI as a continuous variable (Table 2).

308 Table 2: Survey regression coefficients of the association between standardized eating behavioural
 309 traits and BMI as a continuous variable

BMI of individual twins			
TFEQ	β [95% CI]	p-value	n
Cognitive restraint	0.1 [-0.7, 0.8]	0.85	176
Disinhibited eating	1.7 [1.0, 2.5]	<0.001	176
Hunger susceptibility	0.1 [-0.7, 0.9]	0.78	176
DEBQ			
Restrained eating	1.3 [0.6, 2.0]	<0.001	245
External eating	0.2 [-0.4, 0.9]	0.50	248
Emotional eating	0.6 [-0.04, 1.3]	0.07	247
BES			
Binge-eating score	1.8 [1.2, 2.5]	<0.001	268
EDI-2			
Drive for thinness	1.5 [-0.7, 2.3]	<0.001	255
Body dissatisfaction	3.2 [2.5, 3.9]	<0.001	255
Bulimia	0.9 [0.2, 1.5]	0.01	258

310 n=number of individuals, BMI=body mass index, TFEQ=Three Factor Eating Questionnaire,
 311 DEBQ=Dutch Eating Behaviour Questionnaire, BES=Binge-eating Scale, EDI-2=Eating Disorder
 312 Inventory-2, β [95% CI]=regression coefficient with 95% confidence interval from survey regressions.

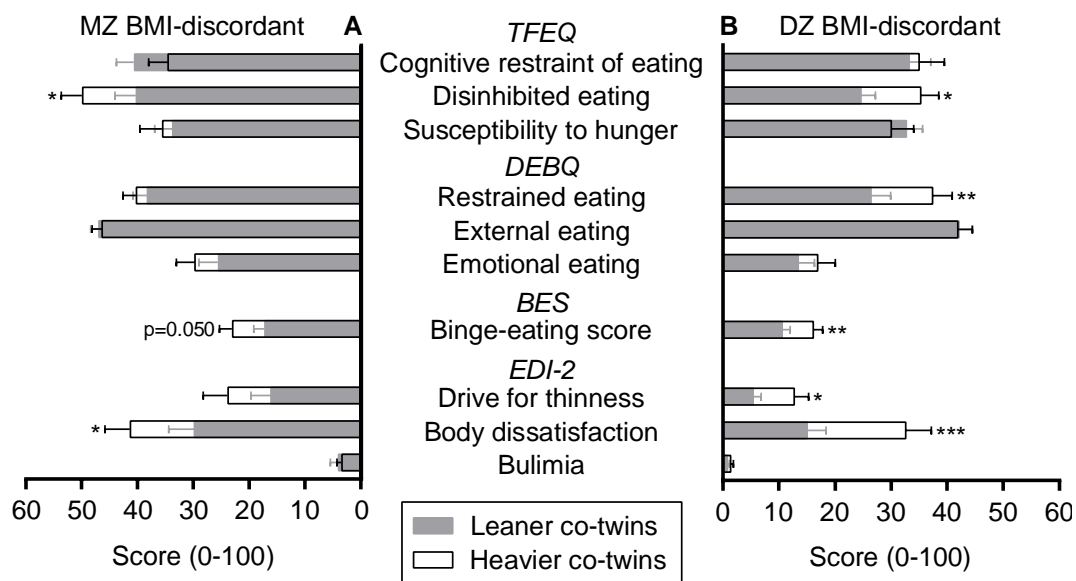
313
 314 In BMI-discordant MZ and DZ twin pairs, evidence was present for higher disinhibited
 315 eating (TFEQ), binge-eating scores (BES; $p=0.050$ in MZ pairs), and body
 316 dissatisfaction (EDI-2) in the heavier co-twins (Figure 2). Only in DZ twins did the
 317 heavier co-twins show higher restrained eating (DEBQ), and drive for thinness (EDI-

318 2). No important intra-pair differences appeared in the BMI-concordant groups
319 (Supplementary Figure S2).

320 The common language effect size for disinhibited eating in MZ BMI-discordant
321 twin pairs was 0.74 [0.57, 0.95] (effect size [95% CI]) and in DZ twin pairs 0.76 [0.62,
322 0.94]. The effect size for binge-eating score in MZ twin pairs was 0.71 [0.50, 1.001]
323 and in DZ twin pairs 0.73 [0.58, 0.92], and for body dissatisfaction in MZ twin pairs
324 this was 0.73 [0.54, 0.99] and in DZ pairs 0.81 [0.72, 0.91].

325 In DZ BMI-discordant female twins, the intra-pair differences in body
326 dissatisfaction and bulimia were significantly larger than in male twins, which were
327 the only sex-differences among all groups (Supplementary Table S6).

328 The behavioural traits had mostly negligible and low intercorrelations (although
329 p-values showed evidence of associations between traits), aside from three moderate
330 correlation coefficients (Supplementary Table S7).

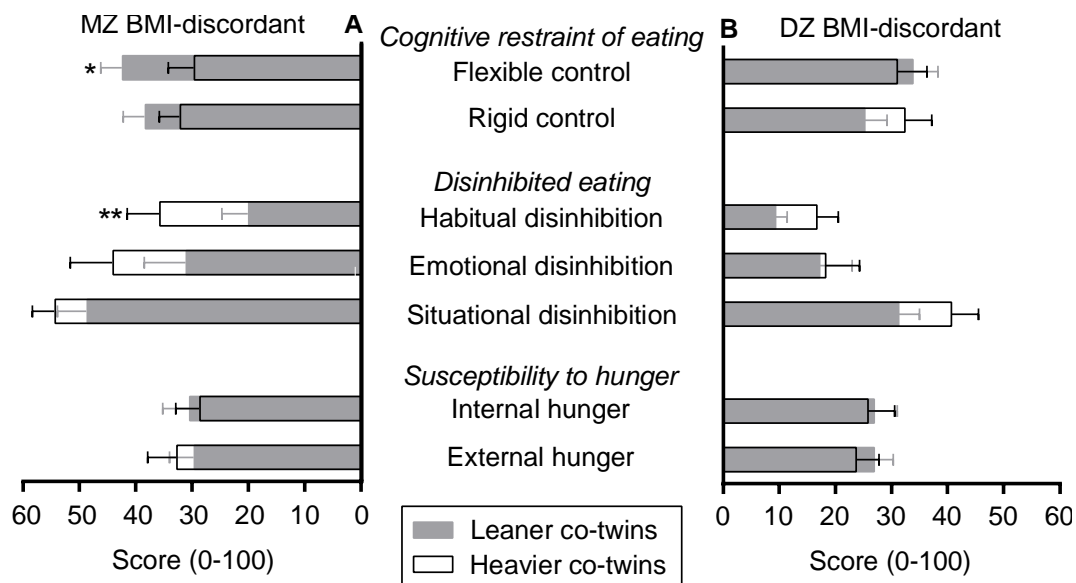


331

332 Figure 2: Overlay bar graph with mean±standard error scores on eating behavioural traits in leaner
 333 and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs discordant for
 334 body mass index (BMI). TFEQ=Three Factor Eating Questionnaire, DEBQ=Dutch Eating Behaviour
 335 Questionnaire, BES=Binge-eating Scale, EDI-2=Eating Disorder Inventory-2. Wilcoxon signed-rank
 336 test *p<0.05, **p<0.01, ***p<0.001.

337

338 After further division of the TFEQ outcome measures into seven subscales (Figure
 339 3), the leaner co-twins of the MZ BMI-discordant twin pairs showed significantly
 340 higher flexible control. The effect size for flexible control was 0.28 [0.08, 0.95]. The
 341 heavier co-twins of this group demonstrated particularly stronger habitual disinhibition
 342 (Figure 3), for which the effect size was 0.78 [0.65, 0.93]. No significant differences
 343 were present in the DZ BMI-discordant twin pairs. In BMI-concordant MZ twin pairs, a
 344 stronger flexible control of the leaner co-twins was found (Supplementary Figure S3),
 345 with an effect size of 0.21 [0.04, 0.99].



346

347 Figure 3: Overlay bar graph with mean±standard error scores on subscales of the Three Factor Eating
 348 Questionnaire in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins
 349 in pairs who are discordant for body mass index (BMI). Wilcoxon signed-rank test *p<0.05, **p<0.01.

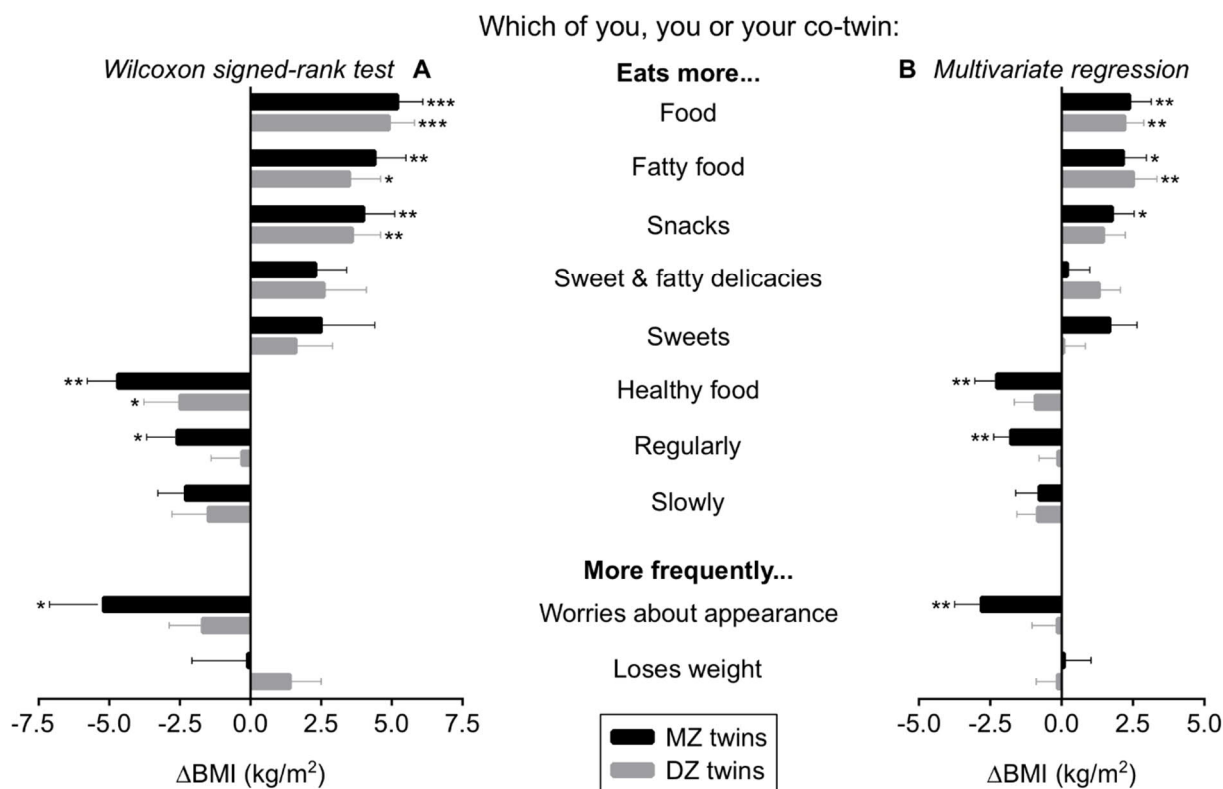
350

351 3.4 Leaner and heavier co-twins' judgment of each others' eating behaviours

352 In the co-twin comparison questionnaire, the twins rated their own eating behaviours
 353 in comparison to their co-twin's eating behaviours (Figure 4), for example, "which of
 354 you (you or your co-twin) eats more?" (Supplementary Text S2). In panel A of Figure
 355 4, the BMIs of only those twin pairs who gave the same, internally consistent
 356 response on which co-twin performs the behaviour more strongly were compared
 357 with the Wilcoxon signed-rank test. The number of twin pairs who agreed on which of
 358 them performed a behavioural trait varied per trait (ranging from 10 to 26 out of 55
 359 MZ and from 13 to 27 out of 65 DZ twin pairs). The strongest significant effects on
 360 BMI were for the MZ twins who ate more food (+5.2 kg/m²), and more fatty food (+4.4
 361 kg/m²), snacks (+4.0 kg/m²), and healthy food (-4.7 kg/m²), and were more worried
 362 about their appearance (-5.2 kg/m²), as well as smaller but significant findings for
 363 eating more sweet and fatty delicacies (+2.3 kg/m²), eating more regularly (-2.6

364 kg/m²), and more slowly (-2.3 kg/m²). In the DZ twins, significant associations with
365 BMI were for eating more food (+4.9 kg/m²), fatty food (+3.5 kg/m²), and snacks (+3.6
366 kg/m²).

367 In panel B of Figure 4, all twin pairs were included for multivariate regression
368 analyses adjusted for age and sex. Intra-pair comparisons of several eating
369 behavioural traits were associated with BMI differences. Eating more food and more
370 fatty food were linked to an intra-pair difference in BMI of +2.3 and +2.4 kg/m² in MZ
371 twins, and +2.3 and +2.6 kg/m² in DZ twins. Furthermore, in MZ twins, eating more
372 snacks was linked to a BMI difference of +1.8 kg/m², whereas eating more healthy
373 food and eating more regularly, as well as being more worried about one's
374 appearance were associated with negative BMI differences (-2.4, -1.8 and -2.7
375 kg/m²).



376

377 Figure 4: (panel A) Wilcoxon signed-rank test was used to compare body mass index (BMI) within
 378 monozygotic (MZ) and dizygotic (DZ) twin pairs who gave an internally consistent answer; (panel B)
 379 Multivariate regression analyses were performed within all twin pairs, and indicated the association
 380 ($\beta \pm$ standard error) between co-twin differences in eating behaviours and intra-pair differences in BMI
 381 (Δ BMI) in kg/m^2 , controlled for age and sex. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

382

383 4. Discussion

384 In both MZ and DZ BMI-discordant twin pairs, the heavier co-twins reported
 385 difficulties regulating their food intake optimally, and they also reported overall
 386 unhealthier eating behavioural traits than did their leaner counterparts. Both twins in
 387 such pairs more frequently agreed that the heavier co-twins ate more food and fatty
 388 food than did their leaner co-twins, and that in MZ twins the heavier co-twins
 389 exhibited an overall unhealthier eating pattern. In BMI-concordant twin pairs, the
 390 leaner and heavier co-twins had comparable eating behaviour. The discussion will
 391 focus on BMI-discordant twin pairs, unless stated otherwise.

392 Initially, we inquired whether the twins were capable of consuming an
393 appropriate amount of food within the twins' perceived requirements. The majority of
394 the heavier MZ and DZ co-twins reported being less capable of eating according to
395 their needs. Instead, they characterized their primary behaviour as frequent
396 overeating, in line with our previous findings (Pietiläinen et al., 2010). Notably, in the
397 current study more than half of the leaner MZ co-twins self-reported non-optimal
398 eating. The reason may be that even the leaner MZ co-twins experienced on average
399 overweight, and perhaps therefore displayed unhealthier behavioural traits. Another
400 preceding investigation of this question demonstrated that both restrictive and
401 overeating behaviours increased the risk for obesity (A. Keski-Rahkonen et al.,
402 2007). Overall, studies in naturalistic settings confirm the common co-occurrence of
403 overeating and restraint, but primarily support the beneficial effects of restraint in
404 reducing overeating and promoting weight loss (Johnson, Pratt, & Wardle, 2012;
405 Schaumberg et al., 2016). The current findings also support the association of
406 overeating, rather than food restriction, with a higher BMI, independent of genotype
407 and shared environment.

408 Augmented disinhibited eating (TFEQ) and binge-eating scores (BES) in the
409 heavier MZ and DZ co-twins further revealed the association between overeating and
410 increased BMI. Disinhibited eating has been linked to BMI (Bryant et al., 2007), and
411 the current study adds evidence for this association independent of genetic and
412 shared environmental factors. Important to note is that the mean value of the binge-
413 eating score implies that the participants are non-bingers. This was in accordance
414 with our exclusion of those with eating disorders. A non-binger might still overeat, but
415 without a dysphoric response (Gormally et al., 1982).

416 Disinhibited eating was divided into habitual, situational and emotional
417 disinhibition subscales (Bond et al., 2001). These provide more detailed information
418 on the nature of disinhibited eating, which may facilitate the tailoring of interventions.
419 Of all seven TFEQ subscales, habitual disinhibition has most strongly predicted
420 weight gain over 20 years (Hays & Roberts, 2008). For us, the heavier co-twins of the
421 BMI-discordant MZ but not DZ twin pairs showed higher habitual disinhibition. Since
422 this finding was not consistent for both zygositys, no inferences on genetic influence
423 are possible.

424 We also investigated two restrictive eating behaviours; restrained eating
425 (DEBQ) and cognitive restraint of eating (TFEQ). Both mainly target restrictions from
426 desired, rather than required, ingestion of food (Lowe & Levine, 2005; van Strien,
427 2008). Hence, high scores on these restraint measures are no guarantee that
428 individuals are restricting their food intake appropriately to lose weight. Furthermore,
429 restrained eating (DEBQ) measures an intention to restrict food intake, whereas
430 cognitive restraint of eating (TFEQ) measures actual caloric restraint (Williamson et
431 al., 2007). We found restrained eating (DEBQ) to characterize the heavier rather than
432 the leaner co-twins of the DZ twin pairs. However, the cognitive restraint of eating
433 (TFEQ) did not differ within the pairs with either of the zygositys. This suggests that
434 the heavier DZ co-twins here had the intention to restrict, but did not actually restrict
435 food intake. Therefore, they might have intended to incorporate restrained eating as
436 a compensatory mechanism for overeating. We cannot, however, exclude the
437 possibility that restrained eating initiated disinhibited eating for those individuals with
438 high scores on both scales (Ouwens, van Strien, & van der Staak, 2003).

439 We divided cognitive restraint of eating (TFEQ) into two subscales; flexible
440 control and rigid control of eating behaviour. Flexible control is a more gradual and

441 subtle approach to limiting food intake than is the all-or-nothing approach of rigid
442 control (Westenhoefer, 1991). Rigid control methods include strict consumption rules,
443 which, when broken, may initiate a loss of control of eating (disinhibited eating).
444 Flexible control is known to be linked with decreased eating behaviour disturbances,
445 decreased body weight, and increased success in weight loss and maintenance, as
446 opposed to the negative health consequences of rigid control (Westenhoefer,
447 Stunkard, & Pudel, 1999). Our findings support the view that flexible control may
448 contribute to the BMI difference, at least within the MZ twin pairs. Flexible control was
449 augmented in the leaner co-twins of the BMI-discordant and -concordant MZ twin
450 pairs, even though the overarching cognitive restraint did not differ within the pairs.

451 The heavier co-twins reported higher body dissatisfaction (in both MZ and DZ
452 pairs), and a stronger drive for thinness (in DZ pairs). Both traits have previously
453 been associated with larger body size (Anna Keski-Rahkonen et al., 2005), and we
454 can complement this with our finding that body dissatisfaction was associated with
455 BMI independent of genotype and shared environment. The intra-pair differences on
456 the EDI-2 questionnaire were significantly larger for DZ females than for males. This
457 was expected, because body dissatisfaction in those who have obesity compared to
458 normal-weight individuals has been recognized to be considerably higher in women
459 than in men (Weinberger et al., 2016).

460 The co-twin comparison questionnaire included both BMI-discordant and
461 concordant twin pairs, and asked all twins to compare their own behaviour with their
462 co-twin's behaviour, as in previous studies (Bogl et al., 2009; Pietiläinen et al., 2010;
463 Rissanen et al., 2002). This approach is advantageous because it provides a
464 verification of behavioural traits by the co-twins, who are reliable proxies of each
465 other's behaviours (Hamilton & Mack, 2000). In our study, the percentage of

466 agreement, within pairs on which co-twin performs which behaviour more strongly is
467 relatively low, this may be because only 2 out of 16 possible answer combinations
468 defined an agreement in the direction of either co-twin. Within the disagreement
469 proportion the answers were diluted over the remaining fourteen answer
470 combinations. Regardless, both MZ and DZ twin pairs agreed more frequently that
471 the heavier co-twin ate more food in general, and more fatty food in particular than
472 their leaner counterparts, in comparison to a vice versa agreement. Additionally, in
473 MZ twins, eating more snacks was associated with a higher BMI, while eating more
474 healthy food, having a regular eating pattern, and being concerned about one's
475 appearance were linked with a lower BMI. Similar behaviours have been associated
476 with BMI in MZ (Bogl et al., 2009; Pietiläinen et al., 2010; Rissanen et al., 2002) and
477 DZ (Bogl et al., 2009) twin pairs. In these studies, no link emerged between eating
478 regularly and BMI, except one reported an association of obesity with a higher intake
479 of sweet and fatty delicacies (Bogl et al., 2009). None of these studies, including
480 ours, found clear differences in BMI based on sweet consumption. Evidence on the
481 associations between sugar intake and body weight remains inconsistent (van Baak
482 & Astrup, 2009).

483 In the food diaries, the leaner and heavier co-twins of the BMI-discordant pairs
484 reported similar dietary intakes, approximately in line with the Nordic Nutrition
485 Recommendations (Nordic Council of Ministers, 2014). However, it is likely that the
486 heavier co-twins significantly underreported, as shown with the doubly labelled water
487 method in our previous sample of BMI-discordant MZ twin pairs (Pietiläinen et al.,
488 2010). Furthermore, undereating during dietary recording periods is a common
489 reason for dietary misreporting, especially by those experiencing obesity (Goris et al.,
490 2000).

491 The current study did not consider energy expenditure, achieved largely
492 through physical activity (PA). In our earlier study, one on PA and metabolic
493 outcomes, we investigated approximately 25 of the same MZ BMI-discordant twin
494 pairs included here (Berntzen et al., 2018). The heavier co-twins took on average
495 nearly 2000 fewer steps per day, and performed approximately 15 minutes less
496 moderate to vigorous PA. Therefore, the PA deficiency in the heavier co-twins likely
497 contributes to the presence of BMI-discordance in these twin pairs. This may also
498 partly explain the lower than expected caloric intake of the heavier co-twins.

499 The current study suggests that a direct question addressing the subjective
500 ability to regulate food intake may be more reliable in screening obesity-related
501 eating patterns in young adults than are food diaries. Additionally, the disinhibited
502 eating measure (TFEQ) might serve as a comprehensive observational tool to
503 capture relevant motives for overeating. Future research should explore the suitability
504 of the food intake regulation question and the disinhibited eating measure for
505 screening and diagnostic purposes, complemented by intervention studies on these
506 behaviours. For example, incorporating a new healthy habit in daily life may diminish
507 habitual disinhibition (Lillis et al., 2016; Rock et al., 2017). Another focus could be on
508 flexible control of eating behaviour, as this was found to diminish the effect of
509 habitual disinhibition on BMI (Hays & Roberts, 2008). Besides this, upcoming studies
510 should try to implement surveys similar to the co-twin comparison questionnaire in
511 populations other than twins; for example through inclusion of individuals who can
512 serve as reliable proxy informants for the eating behaviour of the participants (e.g.,
513 spouse, sibling, other relative, or close friend).

514 This study has strengths and limitations. The design was cross-sectional, so
515 no inferences can be made on causality between eating behaviour and BMI.

516 Information on their socio-economic status was unavailable and was therefore absent
517 as a potential confounder in the models. In general, however, twin pairs have a high
518 concordance for educational attainment and socio-economic status (Marks, 2017;
519 Silventoinen, Kaprio, & Lahelma, 2000). The co-twin control design is unique, but due
520 to the rarity of BMI-discordant pairs the sample size was small (providing low
521 statistical power). Earlier reports on similar eating behaviours in twins who vary in
522 BMI exist, however with even smaller sample sizes (Pietiläinen et al., 2010; Rissanen
523 et al., 2002). We applied more lenient inclusion criteria to reach a larger sample size.
524 Instead of a difference in an internationally defined cut-off point of BMI (e.g. healthy
525 weight vs. obesity), we considered now any minimum of a 3-point difference in BMI
526 important (averaging about 10 kg difference in a person with a height of 170 cm). For
527 example, within the healthy weight category, a BMI of 24 versus a BMI of 20
528 increases risk for type II diabetes (Lehtovirta et al., 2010). Beyond the slightly
529 increased sample size, our study investigated for the first time in such a twin design
530 (to our knowledge) the DEBQ, the comprehensive version of the TFEQ, and the
531 subtypes of behavioural traits from the TFEQ. None of the questionnaires in our
532 study were previously studied in DZ BMI-discordant twin pairs, except the co-twin
533 comparison questionnaire (Bogl. et al 2009). Differences in anthropometry appeared
534 between MZ and DZ twins, possibly explained by a genetic pressure for similarity in
535 MZ pairs. Consequently, discordance in weight is more likely to occur at higher age in
536 MZ pairs. Higher age in itself links with weight gain, which may explain the mild
537 overweight in the leaner co-twins of MZ but not DZ pairs. We performed many tests
538 and reported nominal p-values of the differences with conservative non-parametric
539 tests (Sullivan & Artino, 2013). Perhaps, a multiple testing correction could have been
540 applied. However, we tested behavioural traits only by BMI-discordance, so no

541 exhaustive associations between behaviours and potentially irrelevant outcome
542 measures were performed to force an appearance of low p-values. A multiple testing
543 correction would be overly conservative and could promote type II errors in a small
544 cohort.

545 We included several validated and reliable questionnaires, and were thus able
546 to examine a multitude of eating behavioural aspects within the same research
547 population. This established a robust and comprehensive overview of variations in
548 eating behavioural dimensions associated with BMI-discordance, regardless of
549 numerous personal (age, sex, genes etc.) and shared environmental (*in utero*,
550 childhood, socio-economic, neighbourhood environment) factors.

551

552 **5. Conclusions**

553 Overeating – measured by “frequent overeating”, “disinhibited eating”, and “binge-
554 eating score” – emerged as the main behaviour associated with higher BMI. The
555 twins agreed more frequently that their heavier co-twins habitually ate more food, and
556 particularly more fatty food. Furthermore, the heavier co-twins were generally less
557 satisfied with their bodies. These findings were independent of genetic and shared
558 environmental influences.

559

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573

574 **8. Conflict of Interest**

575 None

576

577 **9. Ethical approval**

578 The authors assert that all procedures contributing to this work comply with the
579 ethical standards of the relevant national and institutional committees on human
580 experimentation and with the Helsinki Declaration of 1975, as revised in 2008.

581 **10. References**

- 582 Altman, D. G., & Bland, J. M. (2011). How to obtain the confidence interval from a P value.
583 *BMJ*, 343, d2090. <https://doi.org/10.1136/bmj.d2090>
- 584 Berntzen, B., Jukarainen, S., Kataja, M., Hakkarainen, A., Lundbom, J., Lundbom, N., ...
585 Pietiläinen, K. (2018). *Physical activity, cardiorespiratory fitness, and metabolic*
586 *outcomes in monozygotic twin pairs discordant for body mass index*. 28(3), 1048–
587 1055.
- 588 Bogl, L. H., Pietiläinen, K. H., Rissanen, A., & Kaprio, J. (2009). Improving the accuracy of
589 self-reports on diet and physical exercise: the co-twin control method. *Twin*
590 *Research and Human Genetics: The Official Journal of the International Society for*
591 *Twin Studies*, 12(6), 531–540. <https://doi.org/10.1375/twin.12.6.531>
- 592 Bohrer, B. K., Forbush, K. T., & Hunt, T. K. (2015). Are common measures of dietary
593 restraint and disinhibited eating reliable and valid in obese persons? *Appetite*, 87,
594 344–351. <https://doi.org/10.1016/j.appet.2014.12.226>
- 595 Bond, M. J., McDowell, A. J., & Wilkinson, J. Y. (2001). The measurement of dietary
596 restraint, disinhibition and hunger: an examination of the factor structure of the
597 Three Factor Eating Questionnaire (TFEQ). *International Journal of Obesity and*
598 *Related Metabolic Disorders: Journal of the International Association for the Study*
599 *of Obesity*, 25(6), 900–906. <https://doi.org/10.1038/sj.ijo.0801611>
- 600 Bryant, E. J., King, N. A., & Blundell, J. E. (2007). Disinhibition: its effects on appetite and
601 weight regulation. *Obesity Reviews: An Official Journal of the International*
602 *Association for the Study of Obesity*, 9(5), 409–419. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-789X.2007.00426.x)
603 [789X.2007.00426.x](https://doi.org/10.1111/j.1467-789X.2007.00426.x)

604 Bublitz, M. G., Peracchio, L. A., & Block, L. G. (2010). Why did I eat that? Perspectives on
605 food decision making and dietary restraint. *Journal of Consumer Psychology, 20*(3),
606 239–258. <https://doi.org/10.1016/j.jcps.2010.06.008>

607 Finnish food composition database. (2009). National Institute for Health and Welfare.
608 Release 9. Helsinki.

609 French, S. A., Epstein, L. H., Jeffery, R. W., Blundell, J. E., & Wardle, J. (2012). Eating
610 behavior dimensions. Associations with energy intake and body weight: a review.
611 *Appetite, 59*(2), 541–549. <https://doi.org/10.1016/j.appet.2012.07.001>

612 Garner, D. M. (1991). *Eating Disorder Inventory-2: professional manual*. Odessa, FL:
613 Psychological Assessment Resources, Inc.

614 Goris, A. H., Westerterp-Plantenga, M. S., & Westerterp, K. R. (2000). Undereating and
615 underrecording of habitual food intake in obese men: selective underreporting of fat
616 intake. *The American Journal of Clinical Nutrition, 71*(1), 130–134.

617 Gormally, J., Black, S., Daston, S., & Rardin, D. (1982). The assessment of binge eating
618 severity among obese persons. *Addictive Behaviors, 7*(1), 47–55.

619 Grimm, E. R., & Steinle, N. I. (2011). Genetics of eating behavior: established and
620 emerging concepts. *Nutrition Reviews, 69*(1), 52–60. [https://doi.org/10.1111/j.1753-](https://doi.org/10.1111/j.1753-4887.2010.00361.x)
621 [4887.2010.00361.x](https://doi.org/10.1111/j.1753-4887.2010.00361.x)

622 Hakala, P., Rissanen, A., Koskenvuo, M., Kaprio, J., & Rönnemaa, T. (1999).
623 Environmental factors in the development of obesity in identical twins. *International*
624 *Journal of Obesity and Related Metabolic Disorders: Journal of the International*
625 *Association for the Study of Obesity, 23*(7), 746–753.

626 Hamilton, A. S., & Mack, T. M. (2000). Use of twins as mutual proxy respondents in a
627 case-control study of breast cancer: effect of item nonresponse and

628 misclassification. *American Journal of Epidemiology*, 152(11), 1093–1103.
629 <https://doi.org/10.1093/aje/152.11.1093>

630 Hays, N. P., & Roberts, S. B. (2008). Aspects of Eating Behaviors “Disinhibition” and
631 “Restraint” Are Related to Weight Gain and BMI in Women. *Obesity (Silver Spring,*
632 *Md.)*, 16(1), 52–58. <https://doi.org/10.1038/oby.2007.12>

633 Hyland, M. E., Irvine, S. H., Thacker, C., Dann, P. L., & Dennis, I. (1989). Psychometric
634 analysis of the Stunkard-Messick Eating Questionnaire (SMEQ) and Comparison
635 with the dutch Eating Behavior Questionnaire (DEBQ). *Current Psychology*, 8(3),
636 228–233. <https://doi.org/10.1007/BF02686751>

637 Johnson, F., Pratt, M., & Wardle, J. (2012). Dietary restraint and self-regulation in eating
638 behavior. *International Journal of Obesity*, 36(5), 665–674.
639 <https://doi.org/10.1038/ijo.2011.156>

640 Jukarainen, S., Heinonen, S., Rämö, J. T., Rinnankoski-Tuikka, R., Rappou, E., Tummers,
641 M., ... Pietiläinen, K. H. (2016). Obesity Is Associated With Low NAD(+)/SIRT
642 Pathway Expression in Adipose Tissue of BMI-Discordant Monozygotic Twins. *The*
643 *Journal of Clinical Endocrinology and Metabolism*, 101(1), 275–283.
644 <https://doi.org/10.1210/jc.2015-3095>

645 Kaprio, J. (2013). The Finnish Twin Cohort Study: an update. *Twin Research and Human*
646 *Genetics: The Official Journal of the International Society for Twin Studies*, 16(1),
647 157–162. <https://doi.org/10.1017/thg.2012.142>

648 Keski-Rahkonen, A., Bulik, C. M., Pietiläinen, K. H., Rose, R. J., Kaprio, J., & Rissanen, A.
649 (2007). Eating styles, overweight and obesity in young adult twins. *European*
650 *Journal of Clinical Nutrition*, 61(7), 822–829. <https://doi.org/10.1038/sj.ejcn.1602601>

651 Keski-Rahkonen, Anna, Bulik, C. M., Neale, B. M., Rose, R. J., Rissanen, A., & Kaprio, J.
652 (2005). Body dissatisfaction and drive for thinness in young adult twins. *The*

653 *International Journal of Eating Disorders*, 37(3), 188–199.
654 <https://doi.org/10.1002/eat.20138>

655 Lauzon, B. de, Romon, M., Deschamps, V., Lafay, L., Borys, J.-M., Karlsson, J., ... Group,
656 F. L. V. S. (FLVS) S. (2004). The Three-Factor Eating Questionnaire-R18 is able to
657 distinguish among different eating patterns in a general population. *The Journal of*
658 *Nutrition*, 134(9), 2372–2380.

659 Lehtovirta, M., Pietiläinen, K. H., Levälähti, E., Heikkilä, K., Groop, L., Silventoinen, K., ...
660 Kaprio, J. (2010). Evidence that BMI and type 2 diabetes share only a minor fraction
661 of genetic variance: a follow-up study of 23,585 monozygotic and dizygotic twins
662 from the Finnish Twin Cohort Study. *Diabetologia*, 53(7), 1314–1321.
663 <https://doi.org/10.1007/s00125-010-1746-4>

664 Lillis, J., Niemeier, H. M., Thomas, J. G., Unick, J., Ross, K. M., Leahey, T. M., ... Wing, R.
665 R. (2016). A randomized trial of an Acceptance Based Behavioral Intervention for
666 weight loss in people with high internal disinhibition. *Obesity (Silver Spring, Md.)*,
667 24(12), 2509–2514. <https://doi.org/10.1002/oby.21680>

668 Loos, R. J. (2018). The genetics of adiposity. *Current Opinion in Genetics & Development*,
669 50, 86–95. <https://doi.org/10.1016/j.gde.2018.02.009>

670 Lowe, M. R., & Levine, A. S. (2005). Eating motives and the controversy over dieting:
671 eating less than needed versus less than wanted. *Obesity Research*, 13(5), 797–
672 806. <https://doi.org/10.1038/oby.2005.90>

673 Lowe, M. R., Whitlow, J. W., & Bellwoar, V. (1991). Eating regulation: The role of restraint,
674 dieting, and weight. *International Journal of Eating Disorders*, 10(4), 461–471.
675 [https://doi.org/10.1002/1098-108X\(199107\)10:4<461::AID-](https://doi.org/10.1002/1098-108X(199107)10:4<461::AID-EAT2260100411>3.0.CO;2-U)
676 [EAT2260100411>3.0.CO;2-U](https://doi.org/10.1002/1098-108X(199107)10:4<461::AID-EAT2260100411>3.0.CO;2-U)

677 Marks, G. N. (2017). The Contribution of Genes and the Environment to Educational and
678 Socioeconomic Attainments in Australia. *Twin Research and Human Genetics*,
679 20(4), 281–289. <https://doi.org/10.1017/thg.2017.32>

680 Mashie FoodTech Solutions AB. (2017). *AivoDiet ver 2.1.0.1*. Malmö, Sweden.

681 McGraw, K. O., & Wong, S. P. (1992). A common language effect size statistic.
682 *Psychological Bulletin*, 111(2), 361–365. [https://doi.org/10.1037/0033-](https://doi.org/10.1037/0033-2909.111.2.361)
683 2909.111.2.361

684 Nordic Council of Ministers. (2014). *Nordic Nutrition Recommendations 2012 : Integrating*
685 *nutrition and physical activity*. Retrieved from
686 <http://urn.kb.se/resolve?urn=urn:nbn:se:norden:org:diva-2561>

687 Ouwens, M. A., van Strien, T., & van der Staak, C. P. F. (2003). Tendency toward
688 overeating and restraint as predictors of food consumption. *Appetite*, 40(3), 291–
689 298.

690 Pietiläinen, K. H., Korkeila, M., Bogl, L. H., Westerterp, K. R., Yki-Järvinen, H., Kaprio, J.,
691 & Rissanen, A. (2010). Inaccuracies in food and physical activity diaries of obese
692 subjects: complementary evidence from doubly labeled water and co-twin
693 assessments. *International Journal of Obesity*, 34(3), 437–445.
694 <https://doi.org/10.1038/ijo.2009.251>

695 Rissanen, A., Hakala, P., Lissner, L., Mattlar, C.-E., Koskenvuo, M., & Rönnemaa, T.
696 (2002). Acquired preference especially for dietary fat and obesity: a study of weight-
697 discordant monozygotic twin pairs. *International Journal of Obesity and Related*
698 *Metabolic Disorders: Journal of the International Association for the Study of*
699 *Obesity*, 26(7), 973–977. <https://doi.org/10.1038/sj.ijo.0802014>

700 Rock, C. L., Flatt, S. W., Nichols, J. F., Pakiz, B., Barkai, H. S., Wing, D. R., ... Buehler, A.
701 E. (2017). Changes in disinhibition, restraint and hunger and associated

702 characteristics during a weight loss intervention. *Journal of Obesity & Weight Loss*
703 *Therapy*, 7(4).

704 Rönnemaa, T., Koskenvuo, M., Marniemi, J., Koivunen, T., Sajantila, A., Rissanen, A., ...
705 Kaprio, J. (1997). Glucose metabolism in identical twins discordant for obesity. The
706 critical role of visceral fat. *The Journal of Clinical Endocrinology and Metabolism*,
707 82(2), 383–387. <https://doi.org/10.1210/jcem.82.2.3763>

708 Schaumberg, K., Anderson, D. A., Anderson, L. M., Reilly, E. E., & Gorrell, S. (2016).
709 Dietary restraint: what's the harm? A review of the relationship between dietary
710 restraint, weight trajectory and the development of eating pathology. *Clinical*
711 *Obesity*, 6(2), 89–100. <https://doi.org/10.1111/cob.12134>

712 Silventoinen, K., Kaprio, J., & Lahelma, E. (2000). Genetic and Environmental
713 Contributions to the Association Between Body Height and Educational Attainment:
714 A Study of Adult Finnish Twins. *Behavior Genetics*, 30(6), 477–485.
715 <https://doi.org/10.1023/A:1010202902159>

716 Stunkard, A. J., & Messick, S. (1985). The three-factor eating questionnaire to measure
717 dietary restraint, disinhibition and hunger. *Journal of Psychosomatic Research*,
718 29(1), 71–83. [https://doi.org/10.1016/0022-3999\(85\)90010-8](https://doi.org/10.1016/0022-3999(85)90010-8)

719 Sullivan, G. M., & Artino, A. R. (2013). Analyzing and Interpreting Data From Likert-Type
720 Scales. *Journal of Graduate Medical Education*, 5(4), 541–542.
721 <https://doi.org/10.4300/JGME-5-4-18>

722 Swinburn, B., Sacks, G., & Ravussin, E. (2009). Increased food energy supply is more
723 than sufficient to explain the US epidemic of obesity. *The American Journal of*
724 *Clinical Nutrition*, 90(6), 1453–1456. <https://doi.org/10.3945/ajcn.2009.28595>

- 725 Timmerman, G. M. (1999). Binge Eating Scale: Further Assessment of Validity and
726 Reliability1. *Journal of Applied Biobehavioral Research*, 4(1), 1–12.
727 <https://doi.org/10.1111/j.1751-9861.1999.tb00051.x>
- 728 van Baak, M. A., & Astrup, A. (2009). Consumption of sugars and body weight. *Obesity*
729 *Reviews: An Official Journal of the International Association for the Study of*
730 *Obesity*, 10 Suppl 1, 9–23. <https://doi.org/10.1111/j.1467-789X.2008.00561.x>
- 731 van Strien, T. (2008). Eating less than required versus eating less than desired. The
732 criterion problem in the validity studies of Williamson et al. (2007). *Appetite*, 50(2–
733 3), 548–549. <https://doi.org/10.1016/j.appet.2007.09.013>
- 734 van Strien, T., Frijters, J. E. R., Bergers, G. P. A., & Defares, P. B. (1986). The Dutch
735 Eating Behavior Questionnaire (DEBQ) for assessment of restrained, emotional,
736 and external eating behavior. *International Journal of Eating Disorders*, 5(2), 295–
737 315. [https://doi.org/10.1002/1098-108X\(198602\)5:2<295::AID-
738 EAT2260050209>3.0.CO;2-T](https://doi.org/10.1002/1098-108X(198602)5:2<295::AID-EAT2260050209>3.0.CO;2-T)
- 739 van Strien, T., Herman, C. P., & Verheijden, M. W. (2012). Eating style, overeating and
740 weight gain. A prospective 2-year follow-up study in a representative Dutch sample.
741 *Appetite*, 59(3), 782–789. <https://doi.org/10.1016/j.appet.2012.08.009>
- 742 Vartanian, L. R., Wharton, C. M., & Green, E. B. (2012). Appearance vs. Health motives
743 for exercise and for weight loss. *Psychology of Sport and Exercise*, 13(3), 251–256.
744 <https://doi.org/10.1016/j.psychsport.2011.12.005>
- 745 Vitaro, F., Brendgen, M., & Arseneault, L. (2009). The discordant MZ-twin method: One
746 step closer to the holy grail of causality. *International Journal of Behavioral*
747 *Development*, 33(4), 376–382. <https://doi.org/10.1177/0165025409340805>
- 748 Weinberger, N.-A., Kersting, A., Riedel-Heller, S. G., & Luck-Sikorski, C. (2016). Body
749 dissatisfaction in individuals with obesity compared to normal-weight individuals: a

750 systematic review and meta-analysis. *Obesity Facts*, 9(6), 424–441.
751 <https://doi.org/10.1159/000454837>

752 Westenhofer, J. (1991). Dietary restraint and disinhibition: Is restraint a homogeneous
753 construct? *Appetite*, 16(1), 45–55. [https://doi.org/10.1016/0195-6663\(91\)90110-E](https://doi.org/10.1016/0195-6663(91)90110-E)

754 Westenhofer, J., Stunkard, A. J., & Pudel, V. (1999). Validation of the flexible and rigid
755 control dimensions of dietary restraint. *International Journal of Eating Disorders*,
756 26(1), 53–64. [https://doi.org/10.1002/\(SICI\)1098-108X\(199907\)26:1<53::AID-
757 EAT7>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1098-108X(199907)26:1<53::AID-EAT7>3.0.CO;2-N)

758 Williamson, D. A., Martin, C. K., York-Crowe, E., Anton, S. D., Redman, L. M., Han, H., &
759 Ravussin, E. (2007). Measurement of dietary restraint: validity tests of four
760 questionnaires. *Appetite*, 48(2), 183–192.
761 <https://doi.org/10.1016/j.appet.2006.08.066>

762 **11. Supplementary material**

763 Supplementary Text S1: Food intake regulation question.

764 Which of the following four alternatives best describes you?

765 1. It is easy for me to eat about the amount I need to → Optimal eating

766 2. I quite often eat more than I actually need → Frequent overeating

767 3. I often try to restrict my eating → Frequent restricted eating

768 4. At times, I'm on a strict diet, at others I overeat → Alternating overeating and restriction

- 769 Supplementary Text S2: Co-twin comparison questionnaire.
- 770 Which of you (you or your co-twin), ...
- 771 – Eats more?
- 772 – Eats more snacks?
- 773 – Eats more fatty foods?
- 774 – Eats more sweet & fatty delicacies (chocolate, pastries, ice cream)?
- 775 – Eats more sweets (candies or jellies)?
- 776 – Selects food more according to healthiness?
- 777 – Eats more regularly?
- 778 – Eats more slowly?
- 779 – Is more worried about appearance?
- 780 – Goes on diets more often?
- 781 Response alternatives: Me, My co-twin, There is no difference between us, Do not know.

782 Supplementary Table S1: Number of twin pairs for whom data is available for the eating behavior
 783 questionnaires.

	BMI-discordant twin pairs		BMI-concordant twin pairs	
	MZ (n=29)	DZ (n=46)	MZ (n=28)	DZ (n=31)
Anthropometry	29	46	28	31
TFEQ				
Cognitive restraint	28	31	15	15
Disinhibited eating	28	31	14	15
Hunger susceptibility	28	31	14	15
DEBQ				
Restrained eating	28	35	28	30
External eating	29	36	28	31
Emotional eating	29	36	28	30
BES				
Binge-eating score	29	46	28	31
EDI				
Drive for thinness	26	40	24	31
Body dissatisfaction	25	44	26	29
Bulimia	26	40	25	30
Food diary	28	35	28	30
Food intake regulation	29	36	24	30
Co-twin comparison	29	35	26	30

784 BMI=body mass index, MZ=monozygotic, DZ=dizygotic, n=total available number of pairs, TFEQ=Three
 785 Factor Eating Questionnaire, DEBQ=Dutch Eating Behavior Questionnaire, BES=Binge-Eating Scale, EDI-
 786 2=Eating Disorder Inventory-2.

787 Supplementary Table S2: Intra-pair differences in characteristics of MZ and DZ twin pairs concordant for BMI.

BMI-concordant twin pairs

	MZ (n=28)				DZ (n=31)			
	Leaner	Heavier	Δ%	p-value	Leaner	Heavier	Δ%	p-value
Age, y	30.3±0.5	30.3±0.5	-	-	28.3±0.4	28.4±0.4	-	-
Female/male, freq.	11/17	11/17	-	-	14/17	14/17	-	-
Height, cm	173.0±1.9	173.5±1.9	0.3	0.26	173.4±1.7	171.8±1.5	-0.9	0.23
Weight, kg	73.7±2.5	77.7±2.5	5.4	<0.001	71.0±2.6	74.6±2.7	5.1	0.002
BMI, kg/m ²	24.5±0.6	25.7±0.6	4.9	<0.001	23.5±0.6	25.2±0.7	7.2	<0.001
Fat mass, kg	19.9±1.4	22.7±1.5	14.1	<0.001*	19.7±1.3	21.6±1.5	9.6	0.02
Body fat, %	26.7±1.7	28.9±1.6	8.2	0.001*	27.4±1.6	28.6±1.7	4.4	0.16

788 Values are mean±standard error. BMI=body mass index, MZ=monozygotic, n=number of pairs, DZ=dizygotic,

789 Δ%=difference in percentages [(heavier-leaner)/leaner×100], freq.=frequency, *n=27 pairs.

790 Supplementary Table S3: Frequencies of BMI category comparisons within twin pairs.

	All twin pairs					
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight	1	2	3	1		
Healthy weight		39	37	10	2	
Overweight			14	12	5	1
Obesity class I				2	3	
Obesity class II						1
Obesity class III						1

	BMI-discordant pairs					
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight			3	1		
Healthy weight		9	31	10	2	
Overweight			1	8	5	1
Obesity class I					2	
Obesity class II						1
Obesity class III						1

	MZ BMI-discordant pairs					
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight						
Healthy weight		1	11	3		
Overweight			1	6	2	1
Obesity class I					2	
Obesity class II						1
Obesity class III						1

791 BMI=body mass index (kg/m²), MZ=monozygotic, DZ=dizygotic, underweight: BMI<18.5; healthy weight: 18.5≤BMI<25; overweight: 25≤BMI<30; obesity
 792 class I: 30≤BMI<35; obesity class II: 35≤BMI<40; obesity class III: BMI≥40.

793 Supplementary Table S3 (continued): Frequencies of BMI category comparisons within twin pairs.

DZ BMI-discordant pairs

	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight			3	1		
Healthy weight		8	20	7	2	
Overweight				2	3	
Obesity class I						
Obesity class II						
Obesity class III						

BMI-concordant pairs

	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight	1	2				
Healthy weight		30	6			
Overweight			13	4		
Obesity class I				2	1	
Obesity class II						
Obesity class III						

MZ BMI-concordant pairs

	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight		1				
Healthy weight		13	4			
Overweight			8	1		
Obesity class I					1	
Obesity class II						
Obesity class III						

794 BMI=body mass index (kg/m²), MZ=monozygotic, DZ=dizygotic, underweight: BMI<18.5; healthy weight: 18.5≤BMI<25; overweight: 25≤BMI<30; obesity
 795 class I: 30≤BMI<35; obesity class II: 35≤BMI<40; obesity class III: BMI≥40.

796 Supplementary Table S3 (continued): Frequencies of BMI category comparisons within twin pairs.

DZ BMI-concordant pairs

	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight	1	1				
Healthy weight		17	2			
Overweight			5	3		
Obesity class I				2		
Obesity class II						
Obesity class III						

797 BMI=body mass index (kg/m²), MZ=monozygotic, DZ=dizygotic, underweight: BMI<18.5; healthy weight: 18.5≤BMI<25; overweight: 25≤BMI<30; obesity

798 class I: 30≤BMI<35; obesity class II: 35≤BMI<40; obesity class III: BMI≥40.

799 Supplementary Table S4: P-values, from an independent samples Mann-Whitney U test for continuous
 800 variables and the Fisher's exact test for categorical variables, of monozygotic versus dizygotic co-twins
 801 (leaner vs. leaner, and heavier vs. heavier) separately for co-twins from body mass index discordant and
 802 concordant pairs.
 803

	BMI-discordant		BMI-concordant	
	Leaner MZ vs. DZ	Heavier MZ vs. DZ	Leaner MZ vs. DZ	Heavier MZ vs. DZ
	co-twins	co-twins	co-twins	co-twins
Age, y	0.03	0.04	0.02	0.02
Female/male, freq.	0.10	0.10	0.79	0.79
Height, cm	0.73	0.37	0.96	0.43
Weight, kg	0.005	0.19	0.34	0.20
BMI, kg/m ²	<0.001	0.02	0.17	0.41
Fat mass, kg	<0.001	0.007	0.76	0.56
Body fat, %	<0.001	0.01	0.56	0.87

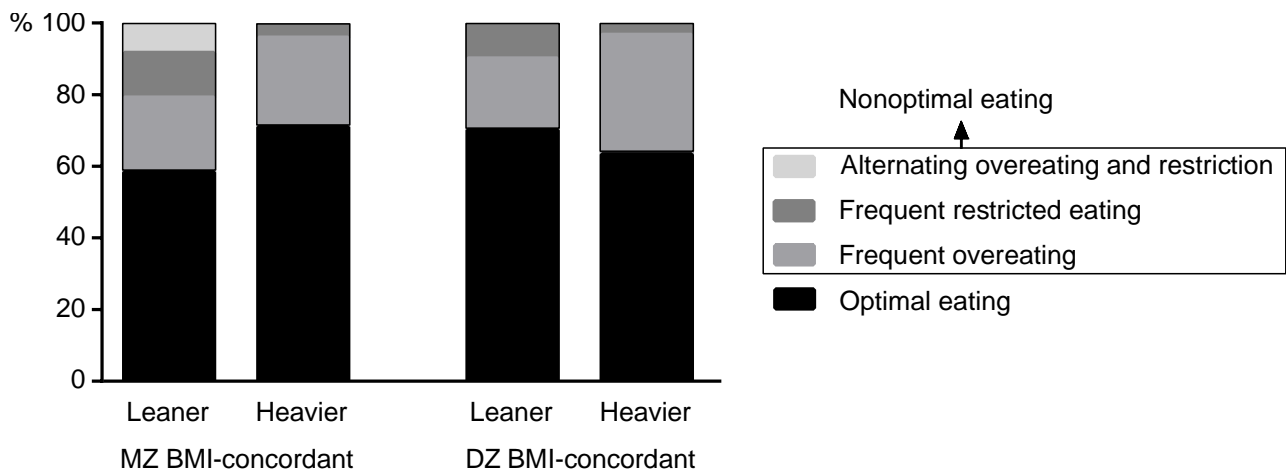
804 BMI=body mass index, MZ=monozygotic, DZ=dizygotic.
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806 Supplementary Table S5: Dietary components in BMI-discordant and -concordant MZ and DZ twins.

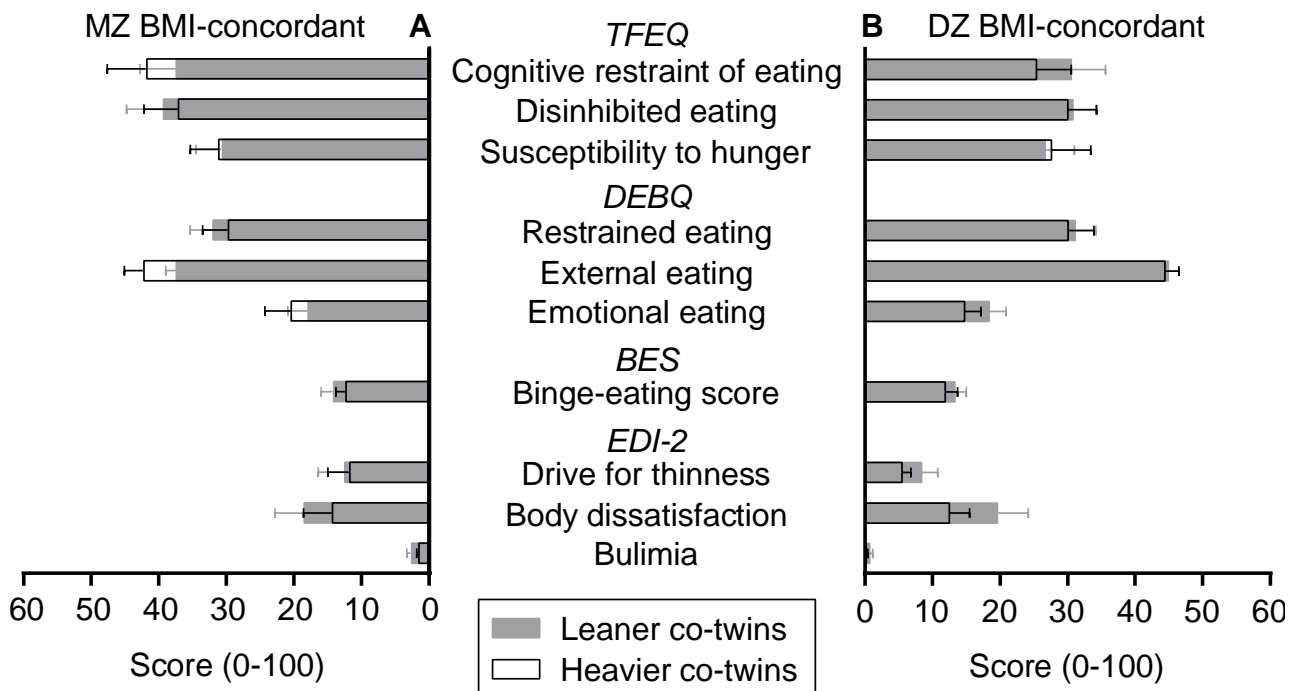
	BMI-discordant twin pairs					
	MZ (n=28)			DZ (n=30)		
	Leaner	Heavier	<i>P</i> -value	Leaner	Heavier	<i>p</i> -value
Total calories, kcal/d	2008±104	2082±115	0.96	2046±91	2201±121	0.31
Carbohydrate, g/d	218.6±11.9	219.1±14.0	0.91	240.0±11.9	266.3±19.4	0.40
Carbohydrate, % energy	43.9±1.3	42.4±1.6	0.18	47.2±1.4	47.5±1.3	0.87
Sugar, g/d	101.4±8.2	103.5±11.8	0.63	100.5±6.5	103.8±8.6	0.90
Sucrose, g/d	51.0±6.0	53.5±9.3	0.80	52.9±5.1	47.9±4.3	0.44
Fructose, g/d	12.6±1.8	14.6±2.0	0.41	11.9±1.3	16.8±2.4	0.28
Protein, g/d	89.7±7.2	89.1±5.8	0.96	88.0±4.4	90.8±5.3	0.73
Protein, % energy	17.8±0.9	17.3±0.6	0.89	17.2±0.5	16.8±0.7	0.68
Fat, g/d	81.1±5.8	84.7±5.2	0.82	78.4±5.5	79.5±4.5	0.62
Fat, % energy	35.7±1.3	36.6±1.3	0.73	33.8±1.4	32.5±1.1	0.53
Saturated fats, g/d	32.6±2.6	31.2±2.1	0.32	30.1±2.4	28.9±1.6	0.96
Alcohol, g/d	7.6±2.2	13.7±3.9	0.53	5.1±1.4	9.5±2.4	0.21
Alcohol, % energy	2.7±1.0	3.8±1.0	0.63	1.8±0.5	3.2±0.8	0.23
Dietary fiber, g/d	17.9±1.7	17.4±1.2	0.84	19.1±1.3	21.9±1.9	0.38

	BMI-concordant twin pairs					
	MZ (n=28)			DZ (n=31)		
	Leaner	Heavier	<i>P</i> -value	Leaner	Heavier	<i>p</i> -value
Total calories, kcal/d	1950±94	2158±101	0.12	2014±108	2279±184	0.50
Carbohydrate, g/d	228.6±13.4	243.0±12.9	0.23	242.9±15.3	272.6±23.3	0.56
Carbohydrate, % energy	46.7±1.6	45.0±1.5	0.23	48.2±1.5	48.0±1.3	0.67
Sugar, g/d	101.9±8.5	97.9±7.6	0.66	100.6±6.9	113.9±9.0	0.31
Sucrose, g/d	53.5±5.5	49.0±4.7	0.49	47.4±5.0	59.2±5.5	0.18
Fructose, g/d	13.4±1.6	11.4±1.3	0.09	13.4±1.6	15.2±2.0	0.53
Protein, g/d	88.3±6.2	96.9±5.1	0.08	84.6±5.1	97.5±12.6	0.83
Protein, % energy	18.0±1.0	18.4±0.9	0.70	17.0±0.7	16.5±0.7	0.36
Fat, g/d	73.3±4.4	81.9±5.0	0.14	72.1±5.0	79.3±6.0	0.39
Fat, % energy	33.5±1.2	33.9±1.5	10.0	31.9±1.2	31.5±1.0	0.67
Saturated fats, g/d	29.6±2.0	29.7±1.9	0.98	26.1±1.9	30.9±2.6	0.08
Alcohol, g/d	4.3±1.8	10.1±4.3	0.59	9.0±2.0	13.3±3.3	0.45
Alcohol, % energy	1.7±0.7	2.7±1.1	0.66	2.9±0.6	4.0±1.0	0.48
Dietary fiber, g/d	18.7±2.0	18.2±1.7	0.95	18.4±1.5	17.9±1.8	0.34

807 Values are mean±standard error. MZ=monozygotic, BMI=body mass index, n=number of pairs, DZ=dizygotic,
808 kcal/d=kilocalories per day, g/d=grams per day, % energy=percentage of total energy intake.



809 MZ BMI-concordant DZ BMI-concordant
 810 Supplementary Figure S1: Percentages of food intake regulation categories in leaner and heavier
 811 monozygotic (MZ) and dizygotic (DZ) twins concordant for body mass index (BMI).



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Supplementary Figure S2: Overlay bar graph with mean±standard error scores on eating behavioral traits in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs concordant for body mass index (BMI). TFEQ=Three Factor Eating Questionnaire, DEBQ=Dutch Eating Behavior Questionnaire, BES=Binge-eating Scale, EDI-2=Eating Disorder Inventory-2.

817 Supplementary Table S6: Intra-pair differences of characteristics and behavioral traits between MZ and DZ
 818 BMI-discordant and -concordant male and female twin pairs.

	MZ BMI-discordant twin pairs			DZ BMI-discordant twin pairs		
	Male (n=10)	Female (n=19)	p-value	Male (n=25)	Female (n=21)	p-value
BMI, kg/m ²	5.7±0.7	6.2±0.7	0.82	6.6±0.7	7.9±0.7	0.08
Fat mass, kg	12.7±2.0	14.2±1.4	0.61	14.8±1.8	18.0±1.9	0.21
Body fat, %	8.2±2.3	9.5±1.1	0.55	12.3±1.7	13.6±1.6	0.87
TFEQ						
Cognitive restraint	-7.1±5.5	-5.3±6.3	0.79	7.8±5.0	-5.4±7.6	0.47
Disinhibited eating	4.4±4.6	12.5±6.8	0.30	5.9±4.7	16.5±5.5	0.24
Hunger susceptibility	1.4±6.0	2.0±6.6	0.55	-3.8±7.6	-1.5±6.7	0.45
DEBQ						
Restrained eating	4.3±4.1	0.8±4.5	0.44	12.6±4.4	8.6±6.5	0.65
External eating	-2.8±3.5	0.5±2.8	0.43	-4.5±3.9	6.0±4.6	0.11
Emotional eating	-.2±7.8	6.6±5.8	0.96	-0.6±3.8	9.4±5.6	0.23
BES						
Binge-eating score	4.3±4.0	6.6±4.6	0.93	3.7±2.3	7.7±3.2	0.28
EDI-2						
Drive for thinness	3.6±3.6	9.5±7.2	0.34	4.2±2.8	12.2±5.8	0.08
Body dissatisfaction	14.6±7.0	9.6±7.0	0.77	8.5±3.5	31.3±8.5	0.01
Bulimia	0.6±1.1	-1.1±2.8	0.75	-0.6±0.6	2.3±1.0	0.02

	MZ BMI-concordant twin pairs			DZ BMI-concordant twin pairs		
	Male (n=17)	Female (n=11)	p-value	Male (n=17)	Female (n=14)	p-value
BMI, kg/m ²	1.1±0.1	1.5±0.3	0.17	1.9±0.2	1.4±0.2	0.09
Fat mass, kg	2.8±0.6	2.7±0.9	1.00	1.6±1.3	2.2±0.7	0.72
Body fat, %	2.2±0.5	2.1±1.4	0.58	.6±1.3	2.0±1.1	0.45
TFEQ						
Cognitive restraint	-11.6±8.4	8.6±8.2	0.12	7.4±7.2	-1.2±5.3	0.69
Disinhibited eating	4.2±8.2	-1.3±4.1	0.74	1.1±5.0	0±9.9	0.95
Hunger susceptibility	2.4±5.6	-5.7±5.2	0.26	1.3±6.9	-7.1±12.4	0.69
DEBQ						
Restrained eating	1.0±4.7	4.1±6.8	0.33	4.3±4.6	-3.3±7.6	0.36
External eating	-4.7±4.0	-5.±3.8	0.71	0±3.7	1.3±3.0	0.97
Emotional eating	1.9±3.7	-9.4±6.0	0.17	8.0±3.7	-1.9±6.0	0.16
BES						
Binge-eating score	3.3±2.1	-0.4±3.3	0.16	1.8±3.1	0.8±3.2	0.69
EDI-2						
Drive for thinness	-2.7±3.8	5.7±4.2	0.14	1.4±2.1	4.8±5.4	0.84
Body dissatisfaction	2.8±2.7	6.3±7.6	1.00	1.6±3.6	13.4±6.4	0.33
Bulimia	2.7±1.9	-1.4±1.6	0.18	-0.3±0.3	1.5±1.0	0.07

819 Values are mean±standard error. MZ=monozygotic, BMI=body mass index, n=number of pairs,
 820 DZ=dizygotic, TFEQ=Three Factor Eating Questionnaire, DEBQ=Dutch Eating Behavior Questionnaire,
 821 BES=Binge-eating Scale, EDI-2=Eating Disorder Inventory-2.

822 Supplementary Table S7: Correlation matrix of individual eating behavioral traits.

Survey		TFEQ			DEBQ			BES	EDI-2		
		Cognitive restraint	Disinhibited eating	Hunger susceptibility	Restrained eating	External eating	Emotional eating	Binge eating score	Drive for thinness	Body dissatisfaction	Bulimia
TFEQ	Cognitive restraint	1.00									
	Disinhibited eating	0.03*	1.00								
	Hunger susceptibility	0.0008	0.28***	1.00							
DEBQ	Restrained eating	0.53***	0.17***	0.007	1.00						
	External eating	0.02	0.26***	0.20***	0.19***	1.00					
	Emotional eating	0.03***	0.54***	0.15	0.16***	0.33***	1.00				
BES	Binge-eating score	0.03*	0.61***	0.22***	0.21***	0.28***	0.32***	1.00			
EDI-2	Drive for thinness	0.15***	0.29***	0.04*	0.26***	0.12***	0.18***	0.39***	1.00		
	Body dissatisfaction	0.05**	0.28***	0.01	0.22***	0.08***	0.16***	0.34***	0.38***	1.00	
	Bulimia	0.0001	0.33***	0.11***	0.02*	0.07***	0.18	0.31***	0.18**	0.11**	1.00

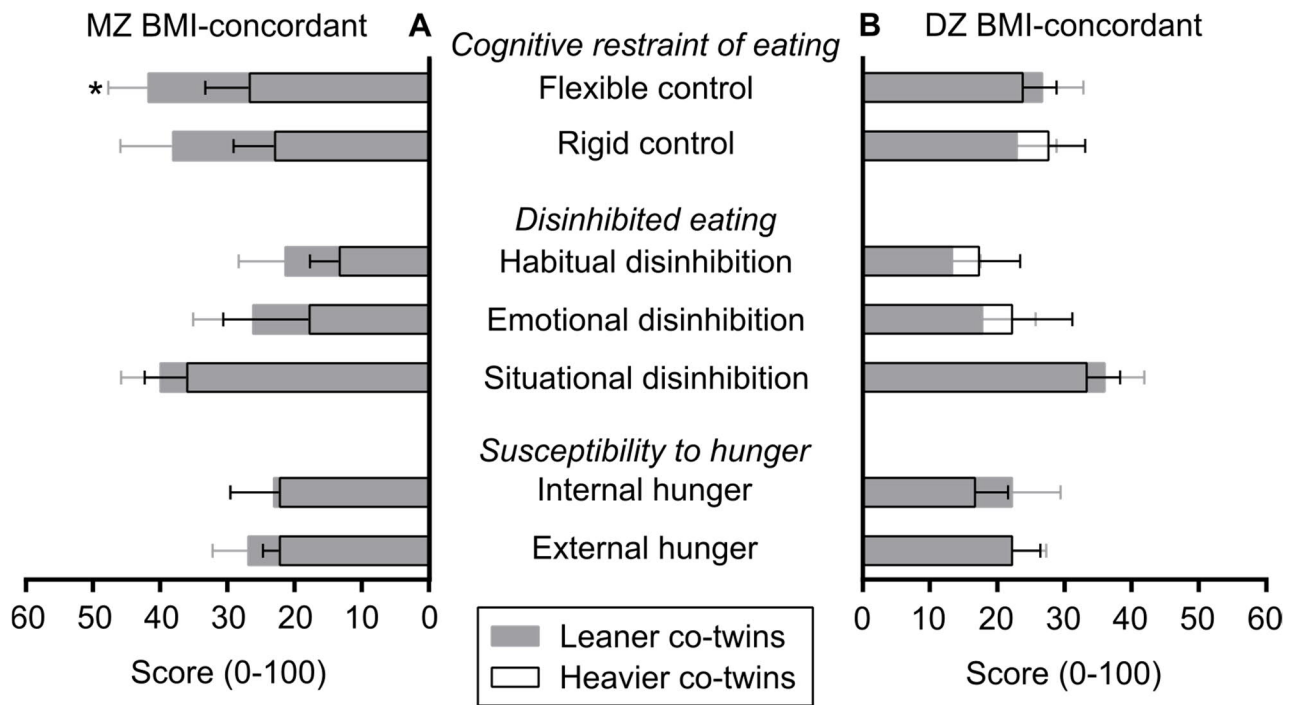
823 TFEQ: Three Factor Eating Questionnaire; DEBQ: Dutch Eating Behavior Questionnaire; BES: Binge-eating Scale; EDI-2: Eating Disorder Inventory-2.

824 Correlation coefficient size (Hinkle et al. 2003): negligible, $r=0.00-0.30$; low, $r=0.30-0.50$; moderate, $r=0.50-0.70$; high, $r=0.70-0.90$; very high, $r=0.90-1.00$.

825 * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

826 Reference: Hinkle DE, Wiersma W, Jurs SG (2003) Applied statistics for the behavioral sciences. Houghton Mifflin, Boston, Mass.; London

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Supplementary Figure S3: Overlay bar graph with mean±standard error scores on subscales of the Three Factor Eating Questionnaire in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs who are concordant for body mass index (BMI). Wilcoxon signed-rank test * $p < 0.05$.