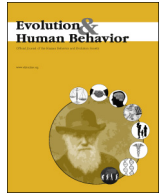




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A test of the facultative calibration/reactive heritability model of extraversion

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ABSTRACT

A model proposed by Lukaszewski and Roney (2011) suggests that each individual's level of extraversion is calibrated to other traits that predict the success of an extraverted behavioral strategy. Under 'facultative calibration', extraversion is not directly heritable, but rather exhibits heritability through its calibration to directly heritable traits ("reactive heritability"). The current study uses biometrical modeling of 1659 identical and non-identical twins and their siblings to assess whether the genetic variation in extraversion is calibrated to variation in facial attractiveness, intelligence, height in men and body mass index (BMI) in women. Extraversion was significantly positively correlated with facial attractiveness in both males ($r = .11$) and females ($r = .18$), but correlations between extraversion and the other variables were not consistent with predictions. Further, twin modeling revealed that the genetic variation in facial attractiveness did not account for a substantial proportion of the variation in extraversion in either males (2.4%) or females (0.5%).

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1. Introduction

Evolutionary psychology has had success in explaining species- and sex- typical psychological adaptations, but less progress has been made towards an evolutionary understanding of individual differences (Buss & Hawley, 2011; Gangestad, 2010; Penke, Denissen, & Miller, 2007; Zietsch, de Candia, & Keller, 2015). Almost all aspects of personality exhibit substantial heritability (the proportion of variation in a trait accounted for by genetic variation), with many studies indicating that around one third to one half of the variation in personality is due to genetic effects (Johnson, Vernon, & Feiler, 2008).

Several genetic and evolutionary models of individual personality differences have been proposed (e.g. Penke et al., 2007), although there have been few empirical tests of these models (Verweij et al., 2012). Natural selection typically works to reduce genetic variation (Barton & Keightley, 2002; Fisher, 1930; Merilä & Sheldon, 1999). Alleles that increase fitness tend to become fixed in the population, while those that reduce fitness are eliminated. Explaining how genetic variation persists despite natural selection is therefore a key theoretical challenge for evolutionary personality psychology. It has been suggested that personality traits are under balancing selection (Penke et al., 2007), in which genetic variation is actively maintained by differential selection pressures. However, more recent research indicates that the genetic

architecture of personality traits is consistent with mutation–selection balance (a balance between accumulation of deleterious mutations and purifying selection against those mutations), rather than balancing selection (Verweij et al., 2012).

Extraversion is widely considered one of the core dimensions of human personality (Ashton, Lee, & Paunonen, 2002; Costa & McCrae, 1992, 1995; Matthews, Deary, & Whiteman, 2009). Extraversion is also associated with a number of behaviors potentially related to fitness. Extraverted individuals engage in sex more frequently, have more extra-pair sexual encounters, and have an increased number of sexual partners overall (Heaven, Fitzpatrick, Craig, Kelly, & Sebar, 2000; Heaven et al., 2003; Nettle, 2005, 2006). In addition, extraversion is associated with higher social status in both men and women (Anderson, John, Keltner, & Kring, 2001), as well as ambition and competitiveness (Nettle, 2005). However, while these behaviors associated with extraversion may serve to enhance fitness, extraverts are also more likely than introverts to incur fitness costs, such as addictions, illnesses, or accidents (Nettle, 2005), or be exposed to communicable diseases (Schaller & Murray, 2008).

The facultative calibration model of extraversion proposes that variation in extraversion is calibrated to variation in other traits that predict the success of an extraverted behavioral strategy (Lukaszewski & Roney, 2011). In this model, extraversion is not directly heritable, but rather exhibits heritability because it is calibrated to individual variation in these other traits, which are themselves directly heritable. This concept is termed "reactive heritability" (Tooby & Cosmides,

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1990). Traits that predict the success of an extraverted behavioral strategy are proposed to be any traits that relate to an individual's 'relative bargaining power'—that is, an individual's ability to extract benefits and inflict costs on other individuals in the social environment. Lukaszewski and Roney proposed physical attractiveness, physical formidability (men only), and intelligence as three traits contributing to relative bargaining power. These traits are assumed to be condition-dependent (i.e. can only reach high levels in individuals of high genetic quality), so the traits' genetic variation is maintained by mutation selection balance.

Lukaszewski and Roney (2011) tested the association of physical attractiveness and physical strength with extraversion, and consistent with their theory found that more attractive individuals and stronger men (but not women) tended to be more extraverted. However, these phenotypic correlations do not necessarily indicate facultative calibration of extraversion to attractiveness or strength. For example, the correlation between extraversion and attractiveness could be the result of other processes, such as social learning. Other individuals evaluate and respond to attractive individuals more favorably from a very young age (Feingold, 1992; Langlois et al., 2000). As such, from early in development, extraverted behaviors of attractive individuals may be reinforced by the actions and responses of their peers (Feingold, 1992), while extraverted behaviors of unattractive individuals receive less social reinforcement and are more often met with rejection. The correlation between extraversion and attractiveness may simply result from general processes of operant conditioning, rather than an evolved mechanism of facultative calibration.

To assess the idea that facultative calibration results in reactive heritability of extraversion, it is an important first step to test the extent to which the genetic variation in extraversion can be accounted for by the genetic variation in traits related to relative bargaining power. We do so in the present study using biometrical modeling on a sample of identical and nonidentical twins who are measured on facial attractiveness, height (related to attractiveness and formidability in men), body mass index (negatively related to attractiveness in women), and intelligence. Data on physical strength are not available for this sample. We briefly provide the rationale behind the measures additional to facial attractiveness:

Height

Height is related to both formidability and attractiveness in men. Taller men are considered to be more attractive than shorter men, are healthier, and are more socially dominant (Blaker et al., 2011; Nettle, 2002; Stulp, Pollet, Verhulst, & Buunk, 2011). In addition, height in men is associated with greater formidability (Fessler, Holbrook, & Snyder, 2012; Sell, Tooby, & Cosmides, 2009), as it is associated with both physical strength and fighting ability (Sell et al., 2008, 2009). As there has been less selection pressure on physical strength or fighting ability in women (Sell et al., 2008), it is not expected that extraversion will be related to height in women. This is consistent with the original findings of Lukaszewski and Roney (2011), who only found a positive relationship between strength and extraversion in men.

Body mass index (BMI)

BMI, measured by an individual's weight divided by their height (squared), accounts for as much as 70% of the variation in female attractiveness (Faries & Bartholomew, 2012; Tovee & Cornelissen, 2001; Tovee, Maisey, Emery, & Cornelissen, 1999). Low BMI (i.e. not overweight) is also associated with health and fertility in women (Lake, Power, & Cole, 1997; Manson et al., 1995). BMI does not have the same strong relationship with attractiveness in men (Maisey, Vale, Cornelissen, & Tovee, 1999).

Intelligence

Intelligence is consistently rated as one of the most important and desirable mate characteristics in both men and women (Buss, 1989; Buss & Barnes, 1986; Li, Kenrick, Bailey, & Linsenmeier, 2002; Shackelford, Schmitt, & Buss, 2005; Stone, Shackelford, & Buss, 2012). Intelligence

reliably predicts success in a variety of domains (Gottfredson, 1997), including better academic and job performance, higher socio-economic status, social success, and ability to acquire resources (Gottfredson, 1997; Kuncel, Hezlett, & Ones, 2004; Prokosch, Coss, Scheib, & Blozis, 2009). Intelligence can be accurately assessed from limited behavioral cues (Borkenau, Mauer, Reimann, Spinath, & Angleitner, 2004), and is likely to be made apparent to others through social interaction. Additionally, individuals with low intelligence are often vulnerable to social exploitation (Gottfredson, 1997), and so may be at a disadvantage if pursuing a highly social strategy such as extraversion. Lukaszewski and Roney (2011) speculated that variation in extraversion should also be calibrated to intelligence, but they did not test this hypothesis.

1.1. The present study

We use a classical twin study ($N = 1659$ individuals) to partition variation in extraversion—and its covariation with facial attractiveness, height, BMI, and intelligence—into genetic and environmental components. In this way we can test the facultative calibration/reactive heritability model's predictions that a substantial amount of the genetic variation in extraversion is accounted for by the genetic variation in facial attractiveness, height (in men), BMI (in women), and intelligence.

2. Method

2.1. Participants

Participants were 1659 individuals from 776 families who took part in the Brisbane Adolescent Twin Study (BATS), which assessed a number of physical, cognitive and psychological outcomes (Wright & Martin, 2004). The present sample consisted of 1455 twins: 142 female monozygotic (MZ) twin pairs and 25 MZ female single twins (whose co-twin did not participate); 112 MZ male pairs and 12 MZ male single twins; 132 dizygotic (DZ) female pairs and 6 DZ female single twins; 101 DZ male pairs and 12 DZ male single twins; and 195 opposite-sex DZ twin pairs with 36 DZ opposite-sex single twins. The single twins were retained in the sample despite the lack of data from their co-twins in order to improve mean and variance estimates. The sample also included 204 non-twin siblings (118 female, 86 male). Twins were tested as closely as possible to their 16th birthday ($M = 16.03 \pm .47$), while their siblings were generally tested at an older age ($M = 17.39 \pm 1.27$).

2.2. Measures

2.2.1. Zygosity

Zygosity in same-sex twins was determined through DNA analysis from blood samples using polymerase chain reaction (PCR) methods. This information was then compared against blood type information and phenotypic information (eye color, hair color) to confirm the zygosity allocation, giving a better than 99% accurate determination.

2.2.2. Extraversion

Personality was measured using either the Junior Eysenck Personality Questionnaire (JEPQ) for participants aged 16 years or under, or the NEO Personality Inventory-Revised (NEO-PI-R) for those seventeen and over. Extraversion scores from each of these measures were separately then standardised (so that both measures are on the same scale) and Winsorised (± 3 SD) to reduce the effects of extreme outliers.

2.2.3. Intelligence

Intelligence was assessed with scores from the verbal intelligence (VIQ) and performance intelligence (PIQ) subscales, as well as the full scale (FIQ) of the Multidimensional Aptitude Battery (MAB). Intelligence scores were also standardised and Winsorised (± 3 SD). For

further details of the recruitment and assessment procedures, see Wright and Martin (2004).

2.2.4. Facial attractiveness

Photographs of participants were taken between 1996 and 2010. Eight undergraduate research assistants (four male and four female) were presented the photographs in random order, and rated each photograph for attractiveness on a seven point scale from 1, low attractiveness, to 7, high attractiveness. Raters were not given any specific instructions or criteria on which to judge attractiveness. Agreement between raters was moderate, intraclass correlation = .44, $p < .001$, and the overall 'scale' reliability was high (Cronbach's $\alpha = .86$). Because the scores of both male and female raters correlated highly with the overall composite score ($r = .94$ and $r = .92$, respectively), the composite score was used in the subsequent analyses (see Lee et al., 2014). As the subjects of more recent photographs tend to be judged as more attractive, the effect of photo year was regressed out of the attractiveness score prior to statistical analysis.

2.3. Statistical analysis

In classical twin design, the observed (phenotypic) variation in a trait can be partitioned into genetic and environmental (non-genetic) sources. Identical (monozygotic, MZ) twins share all their genes, while non-identical (dizygotic, DZ) twins share half their segregating genes on average. Additionally, all twins share the family environment (e.g. prenatal environment, home environment and socioeconomic status). By comparing the similarity of identical and non-identical twins, it is then possible to determine the relative contribution of genetic and environmental factors to the phenotypic variance in a trait.

Genetic sources of variation, A, predict greater similarity between identical twins than non-identical twins. For a trait entirely determined by genetics, we would expect a correlation of 1 between identical twins, and .5 between non-identical twins, corresponding to their genetic similarity. Shared environmental sources of variance, C, predict equal similarity between identical and non-identical twins. For a trait entirely determined by the shared family environment, we would expect a correlation of 1 for both identical and non-identical twins. The residual variance in a trait, E, is attributable to unique environmental experiences, stochastic biological effects, and measurement error, which should be uncorrelated in both identical and non-identical twins. Therefore, the total phenotypic variance in a trait can be partitioned into three sources: additive genetic (A), shared environment (C), and residual/unique environment (E).

The same principles that underlie the univariate twin study also apply to the bivariate design. Fig. 1 shows a Cholesky decomposition, in which latent factor A1 denotes the genetic influences on attractiveness, and the correlated genetic influences on extraversion. The second latent genetic variable, A2, is uncorrelated with latent factor A1, and represents the genetic variation in extraversion that is unexplained by latent factor A1. Corresponding relationships exist for C and E factors.

Analyses were conducted using the Mx matrix algebra software package (Neale, Boker, Xie, & Maes, 2003). Mx uses maximum likelihood modeling to determine the A, C and E parameters that best fit the observed data. Significance of parameters or differences between parameters is tested by dropping or equating relevant model parameters and assessing the change in model fit (distributed as χ^2) against the change in degrees of freedom. Age was modeled as a covariate, controlling for its effects. Male and female parameters were estimated separately. Further details of twin methodology can found elsewhere (Posthuma et al., 2003) and more details of the bivariate

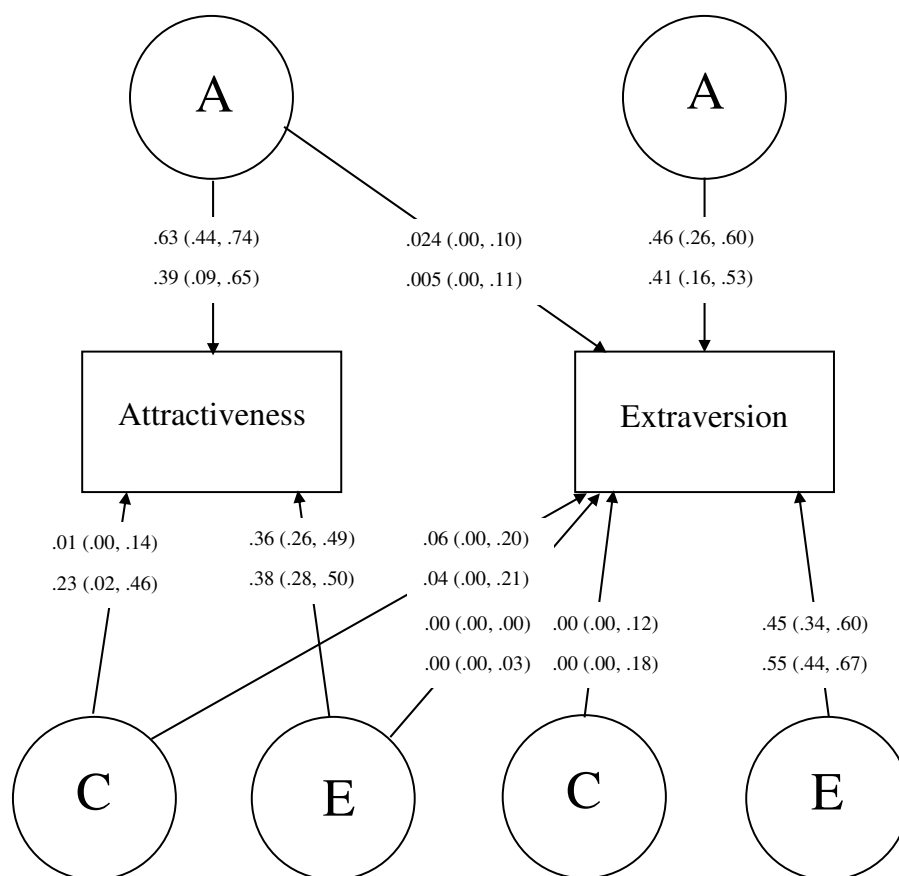


Fig. 1. Path diagram of a bivariate Cholesky decomposition of attractiveness and extraversion, with squared path coefficients for males (upper value) and females (lower value), and 95% confidence intervals. Squared path coefficients represent the proportion of variance in an observed trait accounted for by the latent factor from which the path originates.

Table 1
Proportion of variance in each trait that is accounted for by genetic (A), shared environmental (C), and residual (E) influences (with 95% confidence intervals).

	Extraversion	Attractiveness	Full IQ	Verbal IQ	Perform. IQ	Height	BMI
Males							
A	.55 (.37, .65)	.64 (.37, .75)	.65 (.45, .83)	.61 (.41, .79)	.67 (.36, .81)	.73 (.52, .87)	.82 (.64, .86)
C	.00 (.00, .00)	.02 (.00, .23)	.20 (.02, .38)	.20 (.03, .39)	.08 (.00, .37)	.11 (.00, .31)	.00 (.00, .17)
E	.45 (.35, .58)	.33 (.25, .46)	.16 (.12, .21)	.19 (.15, .25)	.24 (.19, .32)	.15 (.11, .21)	.18 (.14, .24)
Females							
A	.47 (.24, .57)	.40 (.12, .68)	.46 (.27, .68)	.52 (.32, .73)	.66 (.31, .78)	.71 (.53, .91)	.87 (.76, .90)
C	.00 (.00, .17)	.21 (.00, .45)	.33 (.12, .50)	.26 (.07, .44)	.06 (.00, .37)	.20 (.01, .38)	.00 (.00, .10)
E	.53 (.43, .66)	.39 (.30, .50)	.20 (.16, .26)	.22 (.17, .28)	.28 (.22, .36)	.09 (.06, .11)	.13 (.10, .17)

Cholesky decomposition, oriented at the non-expert, can be found in the Supplementary Material of Zietsch, Kuja-Halkola, Walum, and Verweij (2014).

3. Results

3.1. Preliminary analyses

Preliminary testing revealed significantly higher facial attractiveness, performance IQ and full IQ in siblings compared with twins, so sibling and twin means for these variables were not equated in subsequent modeling. However, there were no differences between the correlations of DZ twin and sibling pairs for any trait, concordant with their equal genetic similarity, so these correlations were constrained to be equal in subsequent modeling. It should be noted that the results of subsequent modeling were not substantively different with siblings excluded from the analysis (data not shown).

3.2. Univariate genetic modeling

Table 1 shows A, C, and E estimates for extraversion, facial attractiveness, verbal, performance and full IQ, height, and BMI. All traits were substantially heritable, with much of their variance accounted for by genetic factors.

3.3. Phenotypic correlations

Age-corrected correlations between extraversion, facial attractiveness, verbal, performance and full IQ, height, and BMI are shown in Table 2. There was a modest but significant association between facial attractiveness and extraversion for both males and females, $r = .11$, $p = .008$ and $r = .18$, $p < .001$, respectively. As expected, BMI was significantly negatively correlated with facial attractiveness for both men and women, indicating that individuals with lower BMI are more facially attractive. Also as expected, this correlation was stronger in women ($r = -.32$, $p < .001$) than in men ($r = -.18$, $p < .001$).

Apart from facial attractiveness, only verbal IQ in females was correlated significantly with extraversion ($r = -.07$, $p = .03$), i.e. in the opposite direction to that predicted by the facultative calibration

model. None of the other proposed traits correlated significantly with extraversion. Several other correlations, while weak and nonsignificant, were also in the opposite direction to the predictions of the facultative calibration model.

Only extraversion and facial attractiveness were included in the subsequent genetic analysis, since these were the only variables which showed a significant phenotypic association in the direction predicted by the facultative calibration model.

3.4. Bivariate genetic modeling

Fig. 1 is a path diagram representing the relationships between the observed traits of facial attractiveness and extraversion and the latent genetic, common environmental and residual factors. The genetic variation underlying facial attractiveness only accounted for a small and nonsignificant amount of the variance in extraversion in males (2.4%; $\chi^2_1 = 2.77$, $p = .10$) and females (0.5%; $\chi^2_1 = 0.24$, $p = .63$), respectively.

An alternative way of representing the data is to compare the heritability of extraversion before and after removing the variance shared with facial attractiveness. When the effect of facial attractiveness was regressed out of extraversion, the heritability estimate of extraversion was slightly reduced for both males (.55 to .47) and females (.47 to .43), but the adjusted estimates still fell well within the 95% confidence interval values of the original estimates.

Overall, these results do not support the general prediction that relative bargaining power enhancing traits should increase extraversion. Most relative bargaining power enhancing traits did not correlate with extraversion, or they were associated with lower extraversion. Only facial attractiveness showed the predicted phenotypic correlation with extraversion, but genetic variation underlying facial attractiveness explained no significant variation in extraversion, contrary to the reactive heritability hypothesis.

4. Discussion

The facultative calibration/reactive heritability model predicts that genetic variation in extraversion exists because levels of extraversion are calibrated to variation in other heritable traits that increase the

Table 2
Bivariate correlations between extraversion and relative bargaining power enhancing traits, corrected for age.

	<i>n</i> = 721	<i>n</i> = 623	<i>n</i> = 733	<i>n</i> = 733	<i>n</i> = 733	<i>n</i> = 623	<i>n</i> = 720	Males
	Extraversion	Attractiveness	Full IQ	Perform. IQ	Verbal IQ	Height	BMI	
Extraversion	–	.11** (.03, .19)	–.05 (–.13, .03)	–.01 (–.08, .06)	–.06 (–.13, .01)	–.04 (–.11, .04)	–.08 (–.15, .00)	
Attractiveness	.18** (.12, .25)	–	.01 (–.07, .09)	.02 (–.06, .10)	.00 (–.08, .08)	.00 (–.08, .08)	–.19** (–.26, –.11)	
Full IQ	–.04 (.11, .04)	.02 (–.05, .09)	–	.89** (.87, .90)	.86** (.83, .88)	.18** (.10, .25)	–.01 (–.09, .07)	
Perform. IQ	–.03 (–.10, .04)	.02 (–.05, .09)	.90** (.89, .91)	–	.54** (.49, .59)	.17** (.09, .25)	–.00 (–.07, .07)	
Verbal IQ	–.07* (–.14, –.004)	.01 (–.06, .09)	.84** (.82, .86)	.52** (.47, .57)	–	.14** (.06, .21)	.00 (–.08, .08)	
Height	.05 (–.03, .12)	–.03 (–.10, .04)	.15** (.08, .22)	.13** (.06, .20)	.13** (.07, .21)	–	.05 (–.03, .13)	
BMI	.01 (–.06, .09)	–.32** (–.39, –.25)	–.10** (–.17, –.03)	–.08* (–.15, –.01)	–.09** (–.17, –.02)	.03 (–.05, .10)	–	
Females	<i>n</i> = 882	<i>n</i> = 731	<i>n</i> = 901	<i>n</i> = 901	<i>n</i> = 901	<i>n</i> = 730	<i>n</i> = 881	

* $p < .05$.

** $p < .01$.

relative bargaining power of an individual (and thus increase the success of an extraverted strategy). Here we tested key predictions from this theory: that relative bargaining power enhancing traits are heritable; that extraversion is correlated with relative bargaining power enhancing traits (facial attractiveness, intelligence, height (in men) and low BMI (in women)); and that the genetic variation in extraversion can be accounted for by genetic variation in relative bargaining power enhancing traits.

Overall, the results did not support the facultative calibration/reactive heritability model of extraversion. Unsurprisingly, the relative bargaining power enhancing traits were all substantially heritable, but of these traits, only facial attractiveness correlated with extraversion in the predicted direction. Indeed, several of the correlations were in directions opposite to expectations, one (with verbal IQ in females) significantly. While the significant correlation between extraversion and facial attractiveness was in the direction predicted, analysis of twin data indicated that extraversion was not substantially or significantly influenced by the genetic variation underlying facial attractiveness, contrary to the facultative calibration/reactive heritability model.

Ideally, we could have additionally tested a specific causal prediction of the facultative calibration model with regard to attractiveness: i.e., that genes cause variation in attractiveness which in turn causes variation in extraversion, as opposed to other causal possibilities such as the same (or correlated) genes causing variation in both traits. However, while possible in principle, statistically distinguishing competing causal models with cross-sectional twin data require a much larger sample size and two traits with markedly different heritabilities (Duffy & Martin, 1994), which was not possible given the available data. Nonetheless, such an analysis would not change the results in terms of the proportion or significance of the genetic variation in extraversion that can be explained by facial attractiveness.

There are several plausible explanations for the correlation between extraversion and attractiveness that do not involve facultative calibration. For example: individuals are more responsive to attractive people than unattractive people (Feingold, 1992) and evaluate and treat attractive people more favorably (Langlois et al., 2000). Attractive people may learn that they are more likely to receive a favorable response if they pursue a sociable, extraverted strategy, as the behaviors and expectations of others encourage such sociability (Feingold, 1992). In the absence of similar social reinforcement, or in the presence of social punishment in the form of greater rates of rejection, unattractive people may learn to adopt a more socially withdrawn behavioral strategy. The correlation between extraversion and attractiveness may simply be the result of universal learning processes (operant conditioning), rather than reflecting an evolved mechanism to adaptively optimize extraversion levels. Alternatively or as well, because of their greater social exposure, extraverts may be more likely than introverts to engage in behaviors that increase their facial attractiveness, such as through attention to grooming (Meier, Robinson, Carter, & Hinsz, 2010).

While our results do not provide support for the calibration of extraversion to relative bargaining power enhancing traits in general, it is still possible that extraversion is calibrated to variation in specific traits that we did not measure. Unlike Lukaszewski and Roney (2011), we did not directly test the relationship between physical strength and extraversion, as strength data were not available for the twins and siblings used in this analysis. Although height is related to strength (Sell et al., 2008) and we found no relationship between height and extraversion, it is possible that a direct measure of physical strength (such as chest/arm or hand grip strength) would have yielded different results. Nevertheless, in Lukaszewski and Roney (2011), strength was no stronger a predictor of extraversion than was physical attractiveness, and was only a significant predictor in men, so it seems unlikely that physical strength would explain much of the genetic variation in extraversion.

Another difference between the present study and the original is that we used other-rated facial attractiveness instead of self-rated attractiveness. It could be argued that self-rated attractiveness is a

more appropriate measure for testing the facultative calibration model, as self-rated attractiveness is sensitive to variations in reference class comparisons. However, there is no *a priori* reason to suspect that there are substantial differences in the attractiveness of students from different schools across Brisbane. Furthermore, self-ratings of attractiveness are also likely to be influenced by factors not directly related to attractiveness, such as positive affect. Given the robust association between extraversion and positive affect (Costa & McCrae, 1980; DeNeve & Cooper, 1998; Lucas & Fujita, 2000), the larger correlation between self-rated attractiveness and extraversion observed by Lukaszewski and Roney (2011) could simply be the result of a positivity bias of extraverts, rather than a reflection of the greater relevance of self- than other-rated attractiveness measures.

In summary, the current study used quantitative genetics methodology to assess the facultative calibration/reactive heritability model of extraversion, which predicts that genetic variation in extraversion results from calibration of extraversion to other heritable traits that predict success of an extraverted behavioral strategy. While we corroborated previous findings of a phenotypic correlation between facial attractiveness and extraversion, we found that the genetic factors underlying facial attractiveness had a negligible effect on extraversion. Furthermore, we found no evidence that extraversion is calibrated to other phenotypic traits which would theoretically predict the success of an extraverted behavioral strategy—the relevant traits were either not significantly correlated with extraversion or significantly correlated in the opposite direction to that predicted by the model. Combined, these results cast doubt on facultative calibration as a model for the heritability of individual differences in extraversion.

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