Evolution and Human Behavior 36 (2015) 414–419

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

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

Hannah J. Haysom [a], Dorian G. Mitchem [b,c], Anthony J. Lee [a], Margaret J. Wright [d], Nicholas G. Martin [d], Matthew C. Keller [b,c], Brendan P. Zietsch [a,d,*]

[a] School of Psychology, University of Queensland, Brisbane, Queensland, Australia
[b] Department of Psychology and Neuroscience, University of Colorado Boulder, Boulder, CO, USA
[c] Institute for Behavioral Genetics, University of Colorado Boulder, Boulder, CO, USA
[d] QIMR Berghofer Medical Research Institute, Brisbane, Queensland, Australia

ARTICLE INFO

Article history:
Initial receipt 17 November 2014
Final revision received 5 March 2015

Keywords:
Personality
Facultative calibration
Reactive heritability
Behavior genetics
Relative bargaining power

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%).

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 & McRae, 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,

* Corresponding author.
E-mail address: zietsch@psy.uq.edu.au (B.P. Zietsch).

http://dx.doi.org/10.1016/j.evolhumbehav.2015.03.002
1090-5138/

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 Winsorized (± 3 SD). For