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The Origins of Extraversion: Joint Effects of Facultative Calibration and Genetic Polymorphism

Aaron W. Lukaszewski[1] **and James R. Roney**[1]

Abstract

The origins of variation in extraversion are largely mysterious. Recent theories and some findings suggest that personality variation can be orchestrated by specific genetic polymorphisms. Few studies, however, have examined an alternative hypothesis that personality traits are facultatively calibrated to variations in other phenotypic features, and none have considered how these distinct processes may interact in personality determination. Since physical strength and physical attractiveness likely predicted the reproductive payoffs of extraverted behavioral strategies over most of human history, it was theorized that extraversion is calibrated to variation in these characteristics. Confirming these predicted patterns, strength and attractiveness together explained a surprisingly large fraction of variance in extraversion across two studies—effects that were independent of variance explained by an androgen receptor gene polymorphism. These novel findings initially support an integrative model wherein facultative calibration and specific genetic polymorphisms operate in concert to determine personality variation.

Keywords

extraversion, facultative calibration, personality, behavioral genetics, androgen receptor gene CAG repeat polymorphism

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The extraversion continuum has long been recognized as one of several basic higher order axes of human personality variation, encompassing behavioral facets of sociability, expressiveness, and assertiveness (Wilt & Revelle, 2008). Although much is known about the behavioral and psychophysiological correlates of extraversion (e.g., Botwin & Buss, 1989; Depue & Collins, 1999; Nettle, 2005), much less is understood about the *origins* of individual differences along this dimension. Why do people differ in their levels of extraversion?

Recent theorists have proposed that variation in extraversion reflects trade-offs between its reproductive costs and benefits at different levels along the continuum (Ashton & Lee, 2007; Nettle, 2005). For instance, on the benefit side, extraverted behavior facilitates initiation and maintenance of social relationships (Ashton & Lee, 2007; Nettle, 2005), broadcasts socially valued characteristics to others (Anderson & Shirako, 2008), and promotes social status (Anderson, John, Keltner, & Kring, 2001; Lund, Tamnes, Mouestue, Buss, & Vollrath, 2007). On the cost side, however, extraverted behavior takes up time and energy that could be otherwise expended (Ashton & Lee, 2007), increases one's rate of exposure to communicable diseases (Schaller & Murray, 2008), focuses social attention on one's devalued characteristics (Anderson & Shirako, 2008), and entails high-stakes competition with potentially antagonistic status rivals (Lund et al., 2007). Evidence supports the existence of such trade-offs; for instance, extraverts are more successful on the mating market than introverts but also sustain more serious illnesses and injuries (Nettle, 2005).

If these trade-offs were recurrent across human evolutionary history, then the optimal level of extraversion would have varied for human ancestors as a function of circumstances that reliably modified extraversion's cost–benefit ratio at different points along its continuum. For instance, the optimal level of extraversion may have differed for individuals who varied on other phenotypic features (e.g., physical characteristics) or who found themselves under different socioecological conditions (e.g., high vs. low conflict). It would have been adaptive, therefore, to couple variation in extraversion to the conditions under which different levels were most successful. In general, two possible routes to

[1]University of California, Santa Barbara, CA, USA

Corresponding Author:
Aaron W. Lukaszewski, Haas School of Business, University of California, 545 Student Services #1900, Berkeley, CA 94720-1900
Email: lukaszewski@haas.berkeley.edu

coordination between trait levels and circumstances include: (a) selection for specific polymorphic alleles in response to different conditions and (b) facultative calibration in response to cues available over ontogeny.

Distinct Mechanisms of Personality Determination: Specific Polymorphic Genes Versus Facultative Calibration

Theorists have pointed to the heritability of traits such as extraversion as evidence that between-person variance can ultimately be traced back to specific polymorphic genes, which are posited to encode for the biological substrates of personality (e.g., Bouchard & Loehlin, 2001; Depue & Collins, 1999; Kagan, 1998; McCrae & Costa, 2008; Nettle, 2006; Penke, Denissen, & Miller, 2007). Natural selection can maintain genetic polymorphisms that underlie adaptive trait variation when selection pressures fluctuate across time and space,[1] or when the optimal strategy is frequency dependent[2] (Buss, 1991, 2009; Nettle, 2006; Penke et al., 2007; Sih, Bell, Johnson, & Ziemba, 2004; Tooby & Cosmides, 1990). In either case, the basic evolutionary consequence would be the same: Some individuals are born with genes that systematically bias them toward the development of an extraverted phenotype, and others are born with genes that bias them toward an introverted phenotype. At least broadly consistent with this possibility, recent research has identified polymorphic gene loci that appear to have rather direct influences on some of extraversion's neurocognitive substrates (e.g., Canli, 2008; Ebstein, Benjamin, & Belmaker, 2003).

Tooby and Cosmides (1990), however, described an alternative model of personality determination, wherein individuals may come to differ in their personality traits via facultative calibration of psychological mechanisms in response to cues that are available over ontogeny. In essence, they propose the existence of evolved conditional rules of the form "Given condition *x*, pursue behavioral strategy *y*." In theory, such conditional rules should outcompete genetically fixed strategies by improving the functional match between strategy and circumstance, assuming that particular circumstances did in fact reliably predict the payoffs of alternative strategies over evolutionary time. Importantly, the cues to which behavioral strategies are calibrated may be other phenotypic features. For example, body size has reliably predicted the ability to win physical conflicts in many species (Huntingford & Turner, 1987) and could thus function in a conditional rule that calibrates behavioral aggression. Indeed, two of the few explicit tests of facultative calibration in humans indicate that individual differences in men's anger proneness (Sell, Tooby, & Cosmides, 2009) and physical aggression (Archer & Thanzami, 2007) are calibrated to variation in their physical strength. Crucially, in these examples, since physical strength is itself heritable (Silventoinen, Magnusson, Tynelius, Kaprio, & Rasmussen, 2008), anger and aggression will also exhibit heritability even if there are no polymorphic gene loci that directly influence the neural substrates of these behavioral traits—a phenomenon Tooby and Cosmides (1990) labeled "reactive heritability." Heritability estimates on their own, therefore, cannot differentiate between facultative calibration and more direct genetic determination.

Facultative calibration could be a foundational concept for personality psychology. If it is widespread, then mapping the relevant conditional rules may be indispensible to correctly explaining the origins of variability in human personality traits. Significant functional calibration could likewise entail that many behavioral genetics findings are actually unrecognized examples of reactive heritability. For these reasons, tests of the facultative calibration model may be crucial to determine a basic paradigm for personality psychology and to understand the links between genetic variation and individual differences.

Despite this importance, there are few explicit tests of facultative calibration in the extant personality literature (for exceptions, see Archer & Thanzami, 2007; Sell, Tooby, et al., 2009; Simpson, Gangestad, Christensen, & Leck, 1999), and none that pertain to the broadband personality dimensions that have been a central focus in personality psychology (e.g., the Big Five). Furthermore, although there is some evidence for correlations of polymorphic genes with personality traits, extant research has neither pitted facultative calibration against specific genotypes in the explanation of trait variance nor considered how these two types of mechanisms may interact in personality determination.

Thus, the purpose of the current research is to (a) provide empirical tests of the facultative calibration of extraversion to variation in other phenotypic features (Studies 1 and 2) and (b) provide initial tests of an integrative model wherein facultative calibration and genetic polymorphisms operate in concert to determine extraversion levels (Study 2).

Facultative Calibration of Extraversion

In the current research, it is hypothesized that extraversion is calibrated to variation in physical strength and physical attractiveness. Extraverted behavior involves proactively approaching others, competing for social attention, and assertively pursuing status and influence (Ashton, Lee, & Paunonen, 2002; Lund et al., 2007), which, when successful, generates benefits such as the development of valuable social relationships and the acquisition of social status (Anderson et al., 2001; Ashton & Lee, 2007; Nettle, 2005). Since social status and some relationship types (e.g., mateships) are limited resources, however, extraverted behavior will often expose one to conflicts of interest with others, including antagonistic rivals. Throughout most of human history, the absence of formal legal institutions likely meant that such conflicts involved physical force even more often than they do in modern environments (see Lassek & Gaulin, 2009; Puts, 2010; Sell, Tooby, et al., 2009). At least two lines of evidence support this postulate: First, men have evolved to have approximately 80% more upper-body muscle mass and 90% greater upper-body physical strength than women, which signals an evolutionary history of fairly intense physical contest competition among human males (for reviews, see Lassek & Gaulin, 2009; Puts, 2010). Second, consistent with this, in extant hunter-horticultural societies that resemble human ancestral environments, men with greater upper-body strength and/or fighting ability are more successful in social conflicts (von Rueden, Gurven, & Kaplan, 2008) and achieve higher social status (Chagnon, 1988; Patton, 2000; von Rueden et al., 2008) than weaker men. These lines of evidence suggest that physical conflict has been common enough in human ancestral environments that the costs of extraverted behavior would on average have been lower for physically stronger individuals.

It also follows from these considerations that strength-based conflict resolution has been more prevalent and consequential among men than women over human history, which likely explains why men are on average the more violent sex (Archer, 2009; Puts, 2010). As such, physical strength may have been a more influential determinant of extraversion's cost–benefit ratio among men than women. However, women also resort to physically forceful tactics under some circumstances (Archer, 2009; A. Campbell, 2004), and it is therefore possible that strength has, to some extent, played a role in determining the cost–benefit ratio of extraverted strategies among women as well.

Similar arguments apply to physical attractiveness. Extraverted behavior entails associating widely with others and attracting social attention (Ashton et al., 2002), which can promote relationship initiation and social status if one possesses characteristics valued by others. Research suggests that at least some of the features that define physical attractiveness were likely predictive of health, fertility, or formidability in human ancestral environments (for a review, see Roney, 2009), which may help explain why attractive individuals are preferred as associates for many types of relationships (e.g., Kurzban & Leary, 2001; Sprecher & Regan, 2002), are given preferential treatment in cooperative exchanges (Smith et al., 2009), and tend to have higher social status (Anderson et al., 2001). For these reasons, ceteris paribus, extraverted behavior should provide higher relationship-related returns for more attractive individuals. These higher returns in turn justify the risks of pursuing an extraverted strategy, such as opportunity costs in the currencies of wasted time and energy, increased exposure to pathogens and social conflict, and (especially for less attractive individuals) exploitation by social partners and reputational damage resulting from public social rejection.

Consistent with the expectation of a positive relationship between extraversion and attractiveness, previous studies have found that factor scales including physical attractiveness (as well as behavioral items) are positively correlated with extraversion (e.g., Bourdage, Lee, Ashton, & Perry, 2007) and that facial morphs comprised of extreme extraverts are rated as more attractive than those comprised of extreme introverts (Penton-Voak, Pound, Little, & Perrett, 2006). Additionally, extraversion has been found to correlate positively with facial symmetry, which is one determinant of facial attractiveness (Fink, Neave, Manning, & Grammer, 2005; Pound, Penton-Voak, & Brown, 2007). The current research, however, provides the first explicit tests of whether extraversion is in fact calibrated to natural, continuous variation in overall physical attractiveness.

Study 1

The account of extraversion outlined above predicts the existence of facultative psychological adaptations that embody the decision rules "To the extent that I am [physically stronger than others/more physically attractive than others], pursue an extraverted behavioral strategy." The most straightforward empirical predictions arising from this model are that physical strength and physical attractiveness will exhibit independent positive associations with extraversion (with the former effect potentially restricted to men). Study 1 therefore tests whether scores on extraversion-related personality scales are in fact correlated with measures of physical strength and physical attractiveness.

Method

Participants. Eighty five men (*M* age = 19.70, *SD* = 1.29) and 89 women (*M* age = 18.70, *SD* = 1.21) participated for partial course credit at University of California, Santa Barbara (UCSB).

Measures and Procedures

Participants completed all measures in groups of 1 to 5 same-sex peers. Extraversion scales were completed before measures of physical attractiveness and strength.

Extraversion scales. Items from the following measures were rated on Likert scales ranging from 1 (*not descriptive*) to 7 (*very descriptive*).

IPIP HEXACO Extraversion is a 40-item scale developed by the International Personality Item Pool (IPIP) project (http://ipip.ori.org/) intended to measure the four facets of extraversion identified by Lee and Ashton (2008): *Expressiveness* (e.g., "I talk a lot"), *Liveliness* (e.g., "I am usually active and full of energy"), *Sociability* (e.g., "I enjoy being part of a group"), and *Social Boldness* (e.g., "I have a strong personality"; α = .94).

Social attention was measured by Ashton et al.'s (2002) 13-item scale (e.g., "I avoid drawing attention to myself"; $\alpha = .93$).

Shyness was measured by Cheek and Buss's (1981) 20-item scale (e.g., "I do not find it hard to talk to strangers"; $\alpha = .93$).

Physical attractiveness and physical strength. Self-rated physical attractiveness was measured by three items. The first item was a percentile ranking: "If you were to take a random sample of 100 other people from Santa Barbara of my age and sex, I would be more physically attractive than __ % of them." The other two items were rated on 1-to-7 Likert scales: "How physically attractive are you relative to individuals of your same age and sex?" and "At a normal social gathering, what percentage of women (men) are more physically attractive than you?" These items were *Z*-scored before inclusion in a unit-weighted composite variable ($\alpha = .82$).

Physical strength was measured according to procedures validated with weightlifting machines by Sell, Cosmides, et al. (2009). Two measures of strength were obtained using a Jamar® hydraulic dynamometer: chest/arm strength and grip strength. For chest/arm strength measurement, participants held the dynamometer in front of their chest and pressed inward with both arms until they felt they could not apply additional pressure. For grip strength, participants held the dynamometer at their side and squeezed with their dominant hand until they felt they could not apply additional pressure. Flexed bicep circumference was also included. These three measures were *Z*-scored before inclusion in a unit-weighted composite ($\alpha = .81$).

Although we measured only indices of upper-body strength, research demonstrates that upper-body strength is strongly correlated with lower-body strength (Sell, Cosmides, et al., 2009; Silventionen et al., 2008) and is itself predictive of fighting ability (see Sell, Cosmides, et al., 2009; von Rueden et al., 2008).

Results

Because the three conceptually related extraversion measures completed by participants (HEXACO Extraversion, Social Attention Scale, Shyness) were highly correlated (*r*s > .79 after reverse scoring shyness), these measures were averaged to form an extraversion composite.

As can be seen in Table 1, which presents the zero-order correlations of physical attractiveness and physical strength with the composite and individual extraversion measures, results generally confirmed our hypotheses. Physical attractiveness predicted extraversion in both sexes. Physical strength, on the other hand, robustly predicted extraversion among men, but less so among women. Although this sex specificity of strength's effects on extraversion was tentatively expected, a moderated regression analysis testing the interaction between sex and strength on the extraversion composite did not reach significance, $\beta = .16$, $t(170) = 1.51$, $p = .13$, $sr^2 = .01$.

Table 1. Zero-Order Correlations of Physical Attractiveness and Physical Strength Measures With Extraversion Scales (Study 1)

	Extraversion composite	Social Attention	Shyness	HEXACO Extraversion
Physical attractiveness				
Men	.45***	.43***	−.43***	.41***
Women	.35***	.37***	−.25**	.35**
Physical strength				
Men	.42***	.39***	−.38***	.38***
Women	.17	.21*	.06	.20

Note: The extraversion composite represents an average of scores on the three individual scales (with Shyness reverse scored). HEXACO Extraversion = 40-item scale developed by the International Personality Item Pool (IPIP) project.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

Table 2. The Extraversion Composite Regressed Simultaneously Onto Physical Attractiveness and Physical Strength (Study 1)

	β	*t*	*p*	sr^2
Men (model $R^2 = .29$)				
Physical attractiveness	.35	3.60	.001	.12
Physical strength	.31	3.16	.002	.09
Women (model $R^2 = .17$)				
Physical attractiveness	.37	3.75	.000	.14
Physical strength	.21	2.16	.030	.04

Note: Overall model statistics: men, $F(2, 82) = 16.32$, $p < .001$; women, $F(2, 86) = 8.62$, $p < .001$.

To determine whether the observed associations of attractiveness and strength with extraversion were statistically independent, we conducted multiple regression analyses separately for each sex wherein the composite extraversion variable was regressed onto both predictors simultaneously. As can be seen in Table 2, physical attractiveness and strength were each significant independent predictors of extraversion in both sexes, though for women attractiveness explained over 3 times as much unique variance as did strength.

Discussion

The results of Study 1 are consistent with the existence of facultative psychological adaptations that calibrate levels of extraversion to levels of physical strength and physical attractiveness. An alternative explanation for the observed trait correlations, however, might be the existence of genetic loci that simultaneously influence each of the traits in question, that is, pleiotropic genes (Buss, 2009; Nettle, 2006;

Penke et al., 2007; Sih et al., 2004; Tooby & Cosmides, 1990). If, for instance, there exists a specific polymorphic gene locus with independent influences on *both* extraversion *and* physical strength, the association between these traits could reflect common effects of this pleiotropic gene rather than facultative calibration of extraversion to strength over the course of ontogenetic time. Study 2 examines the influence of a genetic locus that appears as likely as any to have pleiotropic effects on traits such as strength and extraversion—the androgen receptor (AR) gene—as a means of addressing this alternative explanation (see below).

In addition, a potential limitation of Study 1 was its use of a self-rated measure of physical attractiveness rather than third-party ratings. Study 2 was thus also designed to test replication of the findings from Study 1 using both self- and other-rated measures of attractiveness.

Study 2

In Study 2, standardized photos of participants were rated by third parties to form a measure of other-rated physical attractiveness. In addition, since self-rated attractiveness was also measured, this allowed a test of the hypothesis that the predicted effect of other-rated attractiveness on extraversion would be mediated through self-rated attractiveness. Such mediation would in turn validate the attractiveness findings from Study 1.

A broader objective of Study 2 was to test whether pleiotropic effects of the AR gene might explain the correlations between extraversion, strength, and attractiveness rather than, or in addition to, these correlations arising via facultative calibration. If any gene could be expected to pleiotropically influence both physical characteristics and a personality trait, it would likely be a gene that affects hormone activity, since hormones are relatively unique in their ability to have widespread effects on target tissues distributed throughout the brain and body (Penke et al., 2007; Sih et al., 2004). Among the hormones that could coordinate extraversion with strength and/or attractiveness, androgens (e.g., testosterone) are logical candidates. This is because androgens are theorized to promote the investment of energy into traits that facilitate competition for mates, resources, and social status (see Bribiescas, 2001; Ellison, 2001), whether those traits are physical (e.g., skeletal muscle mass; see Bhasin, Woodhouse, & Storer, 2003) or behavioral (e.g., aggressiveness/status seeking; see Archer, 2006; Mazur & Booth, 1998). Any gene that increased the production or phenotypic effects of androgens might therefore produce coordinated effects on both morphological features, such as muscle size and strength (which might also influence attractiveness), and behavioral strategies, such as extraversion, that promote greater status seeking and mating effort.

The AR gene provides a clear example of a locus that influences the phenotypic effects of androgens. Smaller numbers of Cytosine-Adenine-Guanine (CAG) codon repeats in exon 1 of this gene predict both greater expression of AR protein (Choong, Kemppainen, Zhou, & Wilson, 1996) and enhanced transcriptional activity of the AR (Chamberlain, Driver, & Miesfeld, 1994). As a result, men with shorter repeats appear to convert the same levels of androgen into larger physiological effects than do men with longer repeats (B. C. Campbell, Gray, Eisenberg, Ellison, & Sorenson, 2007; Zitzmann & Nieschlag, 2007). Because the AR is expressed in both skeletal muscle (Bhasin et al., 2003) and the brain (Pfaff, 1981), shorter CAG repeats could simultaneously predict both greater strength and higher levels of extraversion. Consistent with this, CAG repeat length has been found to negatively predict men's muscle mass (Nielson et al., 2010), physical strength (Simmons & Roney, 2010), behavioral dominance (Simmons & Roney, 2010), and extraversion as measured by the Karolinska scale (Westberg et al., 2009; but for null findings, see Jonsson et al., 2001; Turakulov, Jorm, Jacomb, Tan, & Easteal, 2004). This positive evidence for effects of the AR on both strength and extraversion makes the AR gene the most likely genetic locus to produce pleiotropic effects that might explain the trait correlations reported in Study 1.

In the present study, AR gene sequence data were available from a sample of men who had been genotyped for a separate study (see Roney, Simmons, & Lukaszewski, 2010) and from whom we collected data on physical strength, physical attractiveness, and self-reported extraversion. If CAG repeat length in the AR gene explains why extraversion is positively correlated with strength and attractiveness, controlling for the influence of AR genotype should produce nonsignificant partial correlations between extraversion and strength/attractiveness. If, on the other hand, strength and attractiveness still predict extraversion independent of any influences of AR genotype, this would support a role for facultative calibration in addition to any direct influences of this genetic polymorphism. Genotype data were not available for women participants in Study 2, and we therefore simply tested replication of the findings from Study 1 (with the addition of the other-rated attractiveness measure) for these participants.

Method

Participants. One hundred forty-six men (M age = 18.90, SD = 1.35) and 52 women (M age = 18.80, SD = 1.17) who were part of a larger study on the biology of mating behavior and personality participated for partial course credit at UCSB.

Materials and procedures. Participants completed all measures in groups of 1 to 5 same-sex peers. The extraversion scale was completed before measures of physical attractiveness and strength. Because of sex-specific protocols in the larger study, we obtained tissue samples for genotyping only from the male sample. Although the male participants also

Table 3. Zero-Order Correlations Among Extraversion and Its Hypothesized Determinants (Study 2)

	Self-rated attractiveness	Other-rated attractiveness	Physical strength	IPIP extraversion
AR CAG repeat length	–.15	–.13	–.23**	–.26**
Self-rated attractiveness	—	.25**	.27**	.36***
Other-rated attractiveness	.49***	—	.26**	.24**
Physical strength	–.08	–.37**	—	.32***
IPIP extraversion	.64***	.34*	.03	—

Note: Correlations for men are above the diagonal; correlations for women are below the diagonal. IPIP = International Personality Item Pool; AR CAG = androgen receptor.
*$p < .05$. **$p < .01$. ***$p < .001$.

participated in a social interaction manipulation (see Roney et al., 2010), that manipulation occurred in a different session separated at least 1 week from the session in which the measures in the current study were collected.

Extraversion was measured by the 10-item scale (e.g., "I start conversations") developed as part of the IPIP project (http://ipip.ori.org/; α = .90).

Self-rated physical attractiveness was measured exactly as in Study 1 (α = .79).

Other-rated physical attractiveness was measured by having participants' photos rated by eight undergraduates at UCSB (five women, three men; *M* age = 20.75, *SD* = .89). Two photos were taken of each participant wearing identical tank-top undershirts with a neutral facial expression: a facial photo and a full upper-body photo, both of which were taken from standardized distances. Once the eight raters had viewed all participant photos to get a sense of the variation in the sample, they rated each participant's photos for facial attractiveness, body attractiveness, and overall physical attractiveness on a 1-7 Likert scale. Agreement was high for facial attractiveness (intraclass correlation coefficient [ICC] = .92), body attractiveness (ICC = .96), and overall physical attractiveness (ICC = .94). Facial, body, and overall attractiveness ratings were highly correlated (*r*s > .71) and were therefore combined into an other-rated attractiveness composite.

Physical strength was measured as in Study 1, except that bicep circumference was not taken. Thus, the strength measure in Study 2 was a two-item composite composed of chest/arm strength and grip strength (α = .71).

AR CAG repeat length was determined by genotyping tissue samples obtained by having participants swish with mouthwash. Mouthwash/expectorate samples were stored at –80°C before being delivered on dry ice to the Biological Samples Processing Core at University of California, Los Angeles (UCLA). After DNA extraction, genotyping and sequencing were carried out by the UCLA Sequencing and Genotyping Core. The forward and reverse primers used in the polymerase chain reaction (PCR) were: 5'-TCCAGAATCTGTTCCAGACGGTGG-3' and 5'-GCTCTGAAGGTTGCTGTTCCTCAT-3'. Roney et al. (2010) describe further details regarding the genotyping procedures.

Mean CAG repeat length among men for whom DNA could be extracted (n = 138) was 21.74 (range = 14-31 repeats). The distribution of CAG repeat lengths was positively skewed and highly leptokurtic, and as such a nonparametric approach to statistical analysis was warranted. To this end, we followed the convention established in many previous studies (e.g., B. C. Campbell et al., 2007; Jonsson et al., 2001; Turakulov et al., 2004; Westberg et al., 2009) of dichotomizing CAG repeat length on the basis of a median split as either short (<22 repeats) or long (≥22 repeats) for data analysis.

Results and Discussion

As can be seen in Table 3, the zero-order correlations among extraversion and its hypothesized determinants were consistent with our hypotheses. Among men, extraversion was positively predicted by self-rated physical attractiveness, other-rated physical attractiveness, and physical strength and was negatively predicted by AR CAG repeat length.[3] Among women, extraversion was positively predicted by both physical attractiveness measures, but strength was uncorrelated with extraversion. In addition, the significance of the sex difference in the effects of strength was tested using moderated regression, which—confirming the trend observed in Study 1—revealed an interaction between strength and sex in the prediction of extraversion, $\beta = .16$, $t(193) = 2.03$, $p = .04$, $sr^2 = .02$.

Self-rated and other-rated physical attractiveness measures were correlated in both sexes (see Table 3), suggesting that participants' internal representations of their own attractiveness are consistent with others' perceptions. Because it could be that the association of self-rated attractiveness and extraversion reported in Study 1 reflected a self-report bias rather than a true association, we tested whether effects of other-rated attractiveness are mediated through self-rated attractiveness. Because the conditions for mediation were met in both men and women, this test was collapsed across data from both sexes. As predicted, Figure 1 demonstrates significant mediation of the effect of other-rated attractiveness on extraversion by self-rated attractiveness. Although the mediation was not entirely complete, it was nearly so, as more than two thirds of the variance common to other-rated

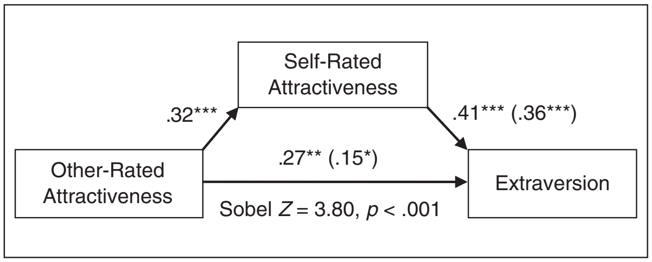

Figure 1. Model testing mediation of the relation of other-rated physical attractiveness with extraversion by self-rated physical attractiveness (collapsed across sex; Study 2)
Note: Values outside parentheses are zero-order βs; values within parentheses are partial βs when both attractiveness measures are entered as simultaneous predictors of extraversion.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

Table 4. Extraversion Regressed Simultaneously Onto Its Hypothesized Determinants (Study 2)

	β	*t*	*p*	sr^2
Men (model R^2 = .23)				
Self-rated attractiveness	.30	3.80	.000	.08
Physical strength	.23	2.86	.005	.04
AR CAG repeat length	–.17	–2.10	.037	.03
Women (model R^2 = .41)				
Self-rated attractiveness	.64	5.76	.000	.41
Physical strength	.08	0.70	.490	.00

Note: Model statistics: men, $F(3, 131) = 13.22$, $p < .001$; women, $F(2, 48) = 16.64$, $p < .001$. AR CAG = androgen receptor.

attractiveness and extraversion was explained through self-rated attractiveness.

Men's physical strength was significantly correlated with both CAG repeat length and physical attractiveness (see Table 3), so it was important to determine whether these variables had independent effects on extraversion. Table 4 confirms that attractiveness, strength, and CAG repeat length each explained unique variance in extraversion when entered simultaneously into a multiple regression analysis, indicating that most of the coordination of extraversion with strength and attractiveness cannot reflect pleiotropic effects of the AR gene (note that results were basically unchanged when self-rated attractiveness was substituted for other-rated attractiveness). Figure 2 further demonstrates that CAG repeat length alone explained a very small fraction of the relation between strength and extraversion (strength's β is reduced from .32 to .29), whereas physical strength partly mediated the effect of repeat length on extraversion. In sum, these patterns support independent effects of attractiveness, strength, and AR genotype on men's levels of extraversion.

As can be seen in Table 4, the conclusions regarding predictors of women's extraversion were not modified by the multiple regression analysis: Physical attractiveness robustly predicted women's extraversion, but strength did not (results were unchanged when self-rated attractiveness was substituted for other-rated attractiveness).

General Discussion

This research tested the hypothesis that individual differences in extraversion are calibrated to variations in physical strength and physical attractiveness, since these characteristics likely predicted the reproductive payoffs of extraverted strategies across most of human history. In support of this, physical attractiveness (for both sexes) and physical strength (primarily among men) exhibited independent positive associations with extraversion, which together explained substantial portions of extraversion's variance across two separate studies. Although theorists have long discussed the importance of testing the facultative calibration model (e.g., Buss, 1991, 2009; Tooby & Cosmides, 1990), the current study is the first to our knowledge that directly tests for facultative calibration of a broadband personality dimension such as extraversion.

Facultative Calibration Versus Pleiotropic Gene Effects

Theorists have also emphasized the importance of testing between distinct mechanisms of personality determination (e.g., Buss, 1991, 2009; Nettle, 2005, 2006; Penke et al., 2007; Sih et al., 2004; Tooby & Cosmides, 1990), but such differential tests have not been forthcoming. The current research took steps in this direction by examining the AR gene CAG repeat polymorphism as a competing determinant of extraversion. Because men's CAG repeat length had effects on both strength and extraversion, this opened the possibility that the association between strength and extraversion reflects pleiotropic effects of this genetic polymorphism on both traits instead of, or in addition to, facultative calibration of extraversion to variation in strength. The overall pattern of results from Study 2 suggests that multiple types of proximate mechanisms may underlie extraversion's origins. Most importantly for the facultative calibration hypothesis, effects of strength and attractiveness remained robust when controlling for men's CAG repeat length, which supports effects of facultative calibration that are independent of the influence of AR genotype.

This research tested only for effects of the AR gene sequence, and thus, it cannot conclusively rule out the existence of other pleiotropic loci that could underlie the observed associations of extraversion with strength and attractiveness. As argued below, however, there are compelling reasons to believe that no pleiotropic gene could do as well as facultative calibration in producing functional matches between behavioral strategies and other phenotypic features. The AR gene was chosen as an extreme test case given its ability to simultaneously influence both brain mechanisms and morphological features, but effects of this gene nonetheless explained negligible fractions of the associations between strength and attractiveness with extraversion.

The generalized reason that no pleiotropic gene is likely to do as well as facultative calibration in explaining personality coordination with morphological features is that traits such as strength and attractiveness are largely dependent on the overall phenotypic condition of the organism[4] (Roney, 2009; Simpson et al., 1999; Tomkins, Radwan, Kotiaho, & Tregenza, 2004), which in turn depends on so many genetic and environmental contingencies that it cannot be reliably predicted from the identity of individual alleles. For instance, attractiveness in part reflects an organism's overall mutation load (see Penke et al., 2007), but individual genes cannot index or appreciably affect this load. As such, no individual gene that directly promoted extraversion could also reliably promote attractiveness.[5] In addition, because pathogens are constantly evolving to exploit different genotypes (see Ridley, 1993; Tooby & Cosmides, 1990), genes that promote good condition at one point may not do so at other times or at other locations. These problems are further compounded by unpredictable ecological factors—such as variable exposure to pathogens and nutrition—that interact with genotypes in complex ways to influence overall condition (e.g., Moller, 2006). In sum, the fact that phenotypic condition is the product of complex interactions between fairly unpredictable genetic and environmental contingencies suggests that pleiotropic gene effects are very unlikely to evolve as sufficiently reliable mechanisms for functionally coordinating personality strategies with condition-dependent traits. By empirically computing one's actual relative standing on traits such as strength and attractiveness, on the other hand, mechanisms of facultative calibration avoid this developmental uncertainty and should therefore produce far more reliable functional matches between behavioral strategies and condition-dependent phenotypic features.

Functional Significance of Men's AR CAG Repeat Polymorphism

Although controlling for AR genotype did not eliminate associations of strength and attractiveness with extraversion, it was nonetheless the case that CAG repeat length still explained unique variance in men's extraversion after controlling for effects of strength and attractiveness (see Table 4 and Figure 2). This is consistent with the possibility that CAG repeat length may have some direct, androgen-mediated effects on extraversion's neural substrates that are not explained via facultative calibration (see also Westberg et al., 2009). What may be happening here is that AR polymorphisms alter the mapping between phenotypic condition

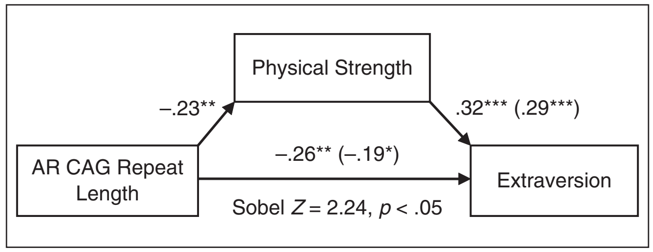

Figure 2. Model testing mediation of the relation of men's androgen receptor CAG repeat length with extraversion by physical strength (Study 2)
Note: Values outside parentheses are zero-order βs; values within parentheses are partial βs when CAG and strength are entered as simultaneous predictors of extraversion.
$^*p < .05$. $^{**}p < .01$. $^{***}p < .001$.

and investment in androgen-dependent traits (see Simmons & Roney, 2010), such that for two men in identical condition, the one with shorter CAG repeat length is more likely to implement an extraverted behavioral strategy. For the reasons argued above, the AR genotype cannot reliably predict condition, but on this account its direct effects on neural mechanisms could potentially explain additional variance in extraversion even after accounting for the effects of facultative calibration.

Polymorphisms in the AR gene, in turn, may have arisen because of differences in the optimal mapping between condition and investment in androgen-dependent traits across different socioecological environments. An important function of androgens in men is to regulate investment of energy into traits that promote successful competition for mates, resources, and social status, which necessarily entails investing less energy in other important metabolic processes such as fat storage and immune function (Bribiescas, 2001; B. C. Campbell et al., 2007; Ellison, 2001; Roney, 2009; Simmons & Roney, 2010). Androgen production itself fluctuates in a condition-dependent manner in men—dropping during illness and energetic stress (see Bribiescas, 2001; Ellison, 2001)—and the number of CAG repeats in the AR gene may in effect act as a dial that adjusts the degree to which condition-indexing androgen concentrations are mapped into phenotypic outcomes. In ecologically harsh or unpredictable environments, this mapping should be more conservative given the greater likelihood of sudden declines in condition, which may select for longer CAG repeats (see B. C. Campbell et al., 2007). Additionally, in social environments with greater polygyny and thus reproductive skew, a stronger mapping of condition into competitive phenotypic traits may be optimal, which would select for shorter CAG repeats. If these speculations are correct, the relations between AR gene polymorphisms and strength/extraversion demonstrated in the present research would represent an empirical confirmation of theorists' suggestions that fluctuating and/or frequency-dependent selection pressures can maintain polymorphic genes that help explain variability in human personality (see Buss, 2009; Nettle, 2005, 2006; Penke et al., 2007; Tooby & Cosmides, 1990).

Implications of Facultative Calibration for the Heritability of Personality Traits

Facultative calibration of behavioral strategy to condition-dependent features has significant implications for explaining the substantial heritability of personality traits. Human physical attractiveness (Rowe, Clapp, & Wallis, 1987) and physical strength (Silventoinen et al., 2008) are both highly heritable, and therefore much of extraversion's demonstrated heritability (Bouchard & Loehlin, 2001) could reflect its calibration to variations in these condition-dependent features. If true, this would exemplify the phenomenon Tooby and Cosmides (1990) labeled "reactive heritability." Under the reactive heritability hypothesis, genetic variance in extraversion does not primarily reflect the existence of "introversion genes" and "extraversion genes" that reliably predict personality across all individuals at all times. Instead, much of extraversion's demonstrated heritability may arise from the operation of universal psychological adaptations (which potentially exhibit zero heritability) that facultatively calibrate extraversion to variations in heritable, condition-dependent traits such as attractiveness and strength.[6]

The reactive heritability argument, however, raises the question of why traits such as strength and attractiveness are heritable, as well as whether specific genes can be found that predict variance in those traits and thus, ultimately, variance in extraversion. The crucial issue here is, once again, the condition dependence of these traits. Phenotypic condition depends on variables such as overall mutation load (e.g., Penke et al., 2007; Tomkins et al., 2004) that are not traceable to specific genes. Likewise, parasite–host coevolution entails that combinations of genes that promote good condition via parasite resistance at one time and place may not do so at other times and places as pathogens adapt to specific gene combinations and thus alter their fitnesses (Ridley, 1993; Tooby & Cosmides, 1990). Chance mutations and pathogen-host arms races thus maintain heritable variation in fitness-related traits because both forces prevent the fixation of a specific set of genes that reliably predicts overall phenotypic condition (see Penke et al., 2007; Tomkins et al., 2004). As such, traits such as strength and attractiveness remain perpetually heritable, even though different combinations of genes predict these outcomes in different individuals across different times and places. This means that facultative calibration of extraversion to strength and attractiveness could involve calibration to traits that have different genetic bases in different persons, such that the reactive heritability of extraversion may not be consistently traceable to polymorphisms in specific genes.

If these arguments are correct, they carry important implications for the field of behavior genetics. This field has recently proceeded by searching for specific polymorphic genes that explain individual differences in specific phenotypic traits. If a substantial fraction of extraversion's heritability is really reactive heritability to condition-dependent traits, though, specific polymorphic genes may turn out to play a minor role in explaining the variance of extraversion. This possibility highlights the importance of incorporating empirical tests of facultative calibration into behavioral genetics research designs to estimate the fraction of heritable variance in personality traits that actually represents reactive heritability to phenotypic condition (e.g., how does the estimated heritability of extraversion change after accounting for the influences of strength and attractiveness?). Our general prediction is that specific gene polymorphisms will be found to explain a relatively small fraction of the total variance in human extraversion (as was the case in the current study for the AR gene), with a larger fraction of the variance explained by various processes of facultative calibration.

Toward an Integrative Model of Extraversion's Origins

The current research illustrates the potential productivity of considering multiple types of proximate and ultimate mechanisms simultaneously in explaining the ontogenetic origins of personality traits. Indeed, across sexes and samples, between 17% and 41% of the variance in extraversion was shown to be explained by models including just two or three hypothesized determinants. Nevertheless, these models leave the majority of extraversion's variance to be explained. In moving toward a framework that comprehensively maps the specific causal antecedents of extraversion, it will be necessary to consider the joint effects of specific genetic polymorphisms and mechanisms of facultative calibration.

Physical strength and attractiveness are but two of numerous phenotypic features according to which extraversion may be facultatively calibrated over ontogeny. Specific candidates for other calibrators of extraversion include characteristics that, like physical strength and attractiveness, help determine one's association value to others. For instance, emerging theories of social status suggest that members of groups confer status on others largely on the basis of their possession of specific intelligences and abilities that predict their capacity to generate collective benefits for the group (Anderson & Kilduff, 2009). Because group members devalue—and even punish—individuals who pursue higher status than others believe they deserve (Anderson, Ames, & Gosling, 2008), it would be adaptive for individual differences in status motivation and extraversion to be facultatively calibrated to variations in status-relevant components of intelligence and ability.

Evolved conditional rules may also calibrate extraversion on the basis of ecological cues. Relevant to this possibility, recent research has demonstrated that cross-national differences in extraversion levels track the worldwide distribution of pathogen prevalence (Schaller & Murray, 2008). Furthermore, these patterns are specific to the prevalence of pathogens that can be transmitted from human to human (Thornhill, Fincher, Murray, & Schaller, 2010), strongly suggesting that they are driven by the disease-related costs of gregarious social strategies that involve interacting with a large number of potential vectors. As these authors point out, it is an empirical question as to whether these personality differences reflect effects of specific polymorphic genes that vary between regions after a history of pathogen-driven genetic evolution pushing populations toward different levels of extraversion, facultative calibration to local pathogen cues, or both. However, recent findings indicate that experimental exposure to disease primes can cause statelike changes in extraversion and approach motivation (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010), suggesting that some variance in extraversion may reflect immediate facultative responses to the current socioecological context.

The current research examined only men's AR CAG repeat polymorphism, but prior studies have identified other specific polymorphic genes that appear to reliably influence extraversion. For instance, extraversion has been associated with several genetic polymorphisms that influence dopamine activity in extraversion's neural substrates (e.g., Canli, 2008; Ebstein et al., 2003). Future research should examine all of these extraversion-related polymorphic genes—and others that may be discovered—in terms of their additive and interactive influences on extraversion, and in terms of their potential interactions with effects of facultative calibration.

As these considerations make clear, a complete picture of the causal processes by which individual differences in extraversion are adaptively determined will likely depict the integration of (a) effects of specific genetic polymorphisms that have been maintained by fluctuating socioecological selection pressures across ancestral populations (e.g., the AR CAG repeat polymorphism), (b) facultative calibration to socioecological cues that have predicted the payoffs of extraverted and introverted behavioral strategies over human history (e.g., cues to local pathogen prevalence), and (c) facultative calibration to other phenotypic features that have predicted the payoffs of extraverted and introverted behavioral strategies over human history (e.g., attractiveness, strength, status-relevant abilities). As such, the construction of a comprehensive model of extraversion's origins will ultimately require that all of these factors be considered in an integrative fashion—especially since facultative calibration and specific polymorphic genes are both viable explanations for heritable personality differences.

Limitations

The current study had certain limitations that suggest directions for future research on the origins of extraversion. First, the claim that physical strength and attractiveness have causal influences on extraversion should be considered along with the caveat that the current study's correlational methods do not conclusively demonstrate this causality. A potential alternative explanation, for instance, is that extraverts are simply more motivated to proactively enhance their strength and attractiveness (e.g., exercise and grooming). However, evidence suggests that muscular body type predicts behavioral disinhibition (a developmental precursor of extraversion) in young boys (Kagan, 1998) and that physically attractive children of both sexes are seen by their peers as socially skilled (Vaillancourt & Hymel, 2006). Unless these extraverted children have been engaging in proactive strength and appearance enhancement, such findings suggest that strength and attractiveness may begin to calibrate extraversion early in development. Future research could address these issues of causality and developmental timescale to further elucidate the specific design features of personality calibration. Another limitation of the current study was the lack of AR CAG repeat data for women. Given the sex-differentiated roles of sex hormones such as androgens (Ellison, 2001), it is unclear whether women's strength and/or extraversion should be predicted by the AR genotype, or by other sex hormone receptor polymorphisms (e.g., estrogen), but these are empirical questions that could be addressed in future research. Finally, the current study exclusively employed self-report scales to measure extraversion, and future studies should therefore attempt to replicate and extend these findings by examining actual behaviors exhibited across functionally distinct types of social contexts.

Conclusion

The present findings demonstrate that a surprisingly large fraction of the between-person variance in extraversion can be predicted from physical strength and physical attractiveness, which in turn provides novel evidence for the facultative calibration of a broadband personality trait. The fact that these effects were shown to be independent of variance explained by the AR gene CAG repeat polymorphism—despite the fact that CAG repeat length had effects on men's strength and extraversion—bolsters the claim that these patterns of multitrait coordination reflect facultative calibration rather than pleiotropic gene effects. Taken together, these findings provide initial support for an integrative model of personality origins wherein facultative calibration and functional genetic polymorphisms operate in concert to determine individual differences. Although our results may be open to alternative explanations, the findings are nonetheless patterns that any complete theory of extraversion's origins must explain, and the data thus carry importance for basic theoretical debates within personality psychology. As such, we hope that this research draws attention to the concept of facultative calibration in the study of personality origins.

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Notes

1. Fluctuating selection occurs when different alleles have the highest fitness at different times and/or places (see Buss, 2009; Nettle, 2006; Penke, Denissen, & Miller, 2007). For instance, selection could promote the spread of genes that promote aggressiveness in some socioecological environments more so than in others, such that genetic polymorphism is observed when measuring across populations or across time within populations. Polymorphism in the genes underlying lactose tolerance (see Bloom & Sherman, 2005) is a concrete example of genetic difference arising from fluctuating selection.
2. Frequency-dependent selection occurs when the reproductive fitness of an allele depends on the frequency of other alleles within a population, such that the evolutionary process maintains multiple alleles in equilibrium (see Buss, 2009; Nettle, 2006; Penke et al., 2007). It has been suggested, for instance, that genes for psychopathy may be in frequency-dependent equilibrium, such that a small percentage of the population can thrive reproductively as psychopaths, but only to the extent that most other people are nonpsychopaths (see Buss, 2009).
3. When men's androgen receptor CAG repeat length was treated as a continuous variable, it still exhibited significant, nonparametric (Spearman) correlations with both physical strength ($\rho = -.22$, $p < .01$) and extraversion ($\rho = -.18$, $p < .05$). Since the dichotomized CAG repeat length variable had larger effects on the relevant traits than the continuous CAG variable, however, the former was more theoretically appropriate for the main analyses. This is because the primary purpose for examining CAG repeat length was to give the alternative "pleiotropy" explanation the best possible chance to compete with the facultative calibration model in explaining the patterns of multitrait association.
4. In evolutionary ecology, "phenotypic condition" essentially refers to a specific individual's ability to convert energy into fitness-promoting traits and outcomes (see Tomkins, Radwan, Kotiaho, & Tregenza, 2004). For instance, an individual with an effective immune system that is well adapted to local pathogens will need to invest less energy in pathogen defense to develop normally and stay healthy than an individual with a lower quality immune system and will therefore have a larger residual energy budget to invest in other fitness-promoting traits such as muscle tissue and attractive morphological ornaments.
5. Notice further that any allele that could reliably promote an outcome such as physical attractiveness would very quickly evolve to fixation in a population, which means that it could no longer explain individual differences. This argument implies that heritable, pleiotropic gene effects that produce between-person correlations between personality and attractiveness are extremely unlikely.
6. It is important to point out that reactive heritability is distinct from the concept of an endophenotype, that is, a lower order substrate of a trait that exists somewhere between genes and a phenotypic outcome (e.g., Canli, 2008). Say, for instance, that alternative alleles for a specific gene alter dopamine metabolism, which evidence suggests is itself an endophenotype of extraversion (Depue & Collins, 1999). One might then validly argue that the heritability of extraversion is derived from the heritability of dopamine metabolism, but this is nonetheless *not* an example of what we mean by reactive heritability, since "dopamine metabolism" and "extraversion" are both aspects of the same underlying trait being described at different levels of analysis (neural endophenotype and behavior, respectively). Reactive heritability, on the other hand, refers to cases in which an adaptive mechanism is designed to adjust a trait (e.g., extraversion) based on other *distinct* phenotypic outcomes that are at least partially heritable (e.g., physical attractiveness).

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