

Heritability of NEO PI-R Extraversion Facets and Their Relationship With IQ

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In recent years, there has been a renewed interest in the relationship between intelligence and personality. Extraversion, in particular, has been suggested to influence intelligence, but the direction of this relationship has been controversial (Wolf & Ackerman, 2005). In a young adult sample, the NEO PI-R was completed by 103 pairs of monozygotic twins, 181 pairs of dizygotic twins and 210 of their nontwin siblings. IQ data (Multidimensional Aptitude Battery) were available for approximately three quarters of this sample, and were collected at 16 years as part of an ongoing study of cognition conducted by the Queensland Institute of Medical Research. All extraversion facets were significantly influenced by genes with both additive and nonadditive genetic effects being important (heritabilities ranged from .25 for activity to .54 for warmth). While a significant correlation between the extraversion domain score and IQ was not found, the extraversion facet of excitement-seeking (E5) was significantly negatively correlated with both verbal ($r = -.15$) and performance ($r = -.11$) IQ scores. The facet of gregariousness was significantly correlated with verbal IQ only ($r = -.09$). The relationship between excitement-seeking and IQ was further shown to be solely due to additive genetic influences. These common genetic effects may stem from a dependence on brain dopamine, a neurotransmitter that has been implicated in both personality and cognition.

The relationship between intelligence and extraversion has been the focus of much research due to Eysenck's (1967, 1994) original hypothesis that introverts had a higher basal arousal level than extroverts and this differentially affected cognitive test-taking performance. In a meta-analysis including over 130 studies, Ackerman and Heggestad (1997) reported a significant, positive correlation between extraversion and general intelligence ($r = .08$). However, an updated meta-analysis (Wolf & Ackerman, 2005), including a more detailed analysis revealed that studies conducted after 2000 support a significant, negative correlation ($r = -.04$). Explanations for this reversal in correlation related to the use of different measurement instruments (the increasing use of the

NEO PI) and the age of participants (negative correlation in older samples). In contrast, there is limited research on the facets (intercorrelated, more narrowly defined traits) of extraversion (as measured by the NEO PI) that have been proposed to be more sensitive to this relationship than the broad personality dimension of extraversion (Allik & Realo, 1997). The present study therefore focuses on the NEO PI-R facets of extraversion in a sample of adolescent and young adult identical and nonidentical twins and their nontwin siblings. The twin design enables the estimation of heritabilities for these measures and the examination of the genetic and environmental covariance between extraversion and IQ.

The heritability of both the broad domain of extraversion and intelligence has been studied extensively. Extraversion shows substantial genetic (~40%) and little shared environmental variation (Aitken Harris et al., 1999; Lynn et al., 1989); several studies also suggest the presence of genetic dominance or epistasis in extraversion (Heath et al., 1992; Jang et al., 1998; Pedersen et al., 1988). The NEO PI facets have been the focus of only a few genetic studies (Jang et al., 1996, 1998, 2002). In a cross-cultural sample of Canadian and German adults ranging 14 to 68 years (mean age of ~30 years) effects of genetic additivity were found for the facets of gregariousness (52%), activity (29%) and positive emotions (39%), and effects of genetic nonadditivity for warmth (43%), assertiveness (42%) and excitement-seeking (41%; Jang et al., 1996). Like extraversion, IQ has been shown to be substantially influenced by genes, with at least half of its variance due to the additive effects of genes (e.g., McClearn et al., 1997; Plomin et al., 2001; Wainwright et al., 2005).

Twin research suggests that the genetic variance in personality and intelligence partly overlaps (Aitken Harris et al., 1998, 1999; Luciano et al., 2006). There is also a priori reason to predict a genetic association between extraversion and IQ based on individual differences in brain dopamine function relating to extraversion and intelligence

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(Previc, 1999; Rammsayer, 1998; Tsai et al., 2002). Dopamine has been proposed as the key neurotransmitter in regulating various cognitive skills critical to human language and thought, including motor planning, working memory and abstract reasoning (Previc, 1999). Dopamine has also been linked to the trait of extraversion, such that introverts show increased levels of dopamine, especially in the caudate nucleus and putamen (Fischer et al., 1997). As greater concentrations of dopamine are linked to higher intelligence and introversion, a negative correlation would be expected between these measures.

The aim of this study is to extend our previous work (Luciano et al., 2004) which found a negative relationship between extraversion (Junior Eysenck Personality Questionnaire) and both verbal and performance IQ scores (Multidimensional Aptitude Battery; Jackson, 1998). Here, we focus on the facet measures of the NEO PI-R and their relationship with IQ; almost half of the sample in the present study overlaps with that of our previous study. Consistent with our previous findings it is hypothesized that a negative correlation between IQ and the extraversion facets will be found, although the strength of this correlation may differ between facets. Based on findings that independently link dopamine with the extraversion trait and intelligence, we expect this relationship to be genetically mediated.

Materials and Methods

Participants

The participants were part of a longitudinal twin family study being conducted at the Queensland Institute of Medical Research and were recruited mostly via primary and secondary schools in South East Queensland and word-of-mouth. Specifically, this sample of twins and their nontwin siblings was involved in the ongoing Cognition (or Memory, Attention, and Problem Solving [MAPS]) study beginning in 1996 (Wright et al., 2001), and a Mail and Phone study conducted in 2002 (Wright & Martin,

2004). IQ data of 16-year-old twins (their siblings were 17 years on average) were obtained from the MAPS study, while extraversion data were primarily collected through a Mail and Phone study later completed when participants were aged 17 to 28 years (mean of 20.2 ± 2). The longest interval between IQ and NEO PI-R data collection was 8 years, with the mean interval being 3 years (standard deviation of 2). For a small subsample, IQ and extraversion data were collected together as part of a new protocol introduced into the MAPS study. Written informed consent was obtained from each participant and their parent/guardian prior to testing. See Wright et al. (2001) and Wright and Martin (2004) for more information about the testing protocols.

Zygosity Testing

The zygosity of same-sex twins was established by typing nine independent DNA microsatellite polymorphisms (polymorphism information content $> .7$) by polymerase chain reaction. Those results were cross-checked with blood group results (ABO, MNS, and Rh; blood typing provided by Australian Red Cross Blood Service, Brisbane), and phenotypic data (hair, skin, eye color). The overall probability of correct zygosity assignment was greater than 99.9% (Nyholt, 2006).

Extraversion Measures

Extraversion data were obtained using the NEO PI-R, which measures each domain of the five-factor model of personality: neuroticism, extraversion, openness, agreeableness and conscientiousness (Costa & McCrae, 1985). The full version of the NEO PI-R contains 240 items, and was completed by participants at home, as part of the Mail and Phone Study. This version generates six facet scores for each domain, so that more narrowly defined aspects of each domain can be investigated. A total of 1406 individuals were sent the NEO PI-R as part of the Mail and Phone study, although this written questionnaire was later made available on the internet. Complete

Table 1

Number of Twins and Siblings (Grouped by Zygosity) with NEO PI-R Domain Scores

Zygosity	Paired sets of twins	Unpaired twins [^]	Siblings of twins (male or female)
1. MZ Female	60	19	26
2. MZ Male	43	18	19
3. DZ Female	53 [†]	17	20
4. DZ Male	42	14	17
5. DZ OS, Female 1 st born	41	24	17
6. DZ OS, Male 1 st born	45 [‡]	22	21
7. Siblings of twins*	—	—	90
Total	284	115	210

Note: OS = opposite-sex

* No twin data collected yet (twins too young)

[^] Where only 1 member of a twin pair was measured.

[†] Includes 2 sets of trizygotic triplets (all female); [‡] Includes 1 set of trizygotic triplets (2 male, 1 female)

Table 2

Descriptive Statistics (Mean, Standard Deviation, Range) of Extraversion Measures, their Maximum Likelihood Co-Twin Correlations (with 95% Confidence Interval), and Pearson Correlations (*r*) between Extraversion Measures and Verbal (VIQ) and Performance IQ (PIQ)

	<i>N</i>	Mean (<i>SD</i>)	Range		Twin correlations (95% CI)		<i>r</i> (<i>p</i> value)	
			Min	Max	MZ	DZ/Sibling	VIQ	PIQ
E Domain (z score) [†]	882	.01 (.99)	-3.52	2.79	.45 (.26, .58)	.07 (-.02, .16)	-.02 (.63)	-.05 (.24)
Warmth (E1)	775	22.35 (4.14)	6	32	.56 (.39, .67)	.08 (-.02, .19)	-.06 (.18)	-.04 (.32)
Gregariousness (E2)	778	19.15 (4.97)	2	32	.27 (.07, .45)	.11 (0, .21)	-.09 (.05)*	-.08 (.06)
Assertiveness (E3)	778	16.10 (5.00)	3	31	.35 (.14, .51)	.06 (-.04, .17)	.02 (.58)	-.04 (.32)
Activity (E4)	777	17.40 (3.78)	8	30	.32 (.08, .50)	.02 (-.09, .13)	.02 (.57)	-.02 (.67)
Excitement-Seeking (E5)	780	21.28 (4.30)	4	32	.32 (.14, .47)	.08 (-.03, .20)	-.15 (.00)**	-.11 (.01)**
Positive Emotions (E6)	779	21.15 (4.60)	2	32	.49 (.31, .62)	.09 (-.02, .21)	.06 (.17)	-.01 (.74)

Note: * $p < .05$; ** $p < .01$

[†]60-item NEO: $N = 109$, range 15 - 45, mean 31.9 (± 5.1); 240-item NEO: $N = 773$, range 54 - 173, mean 117.5 (± 18.5)

Outlying scores (z-score < -3.29 or > 3.29) were excluded from analysis.

data were received from approximately 56%, including 6% who did the questionnaire online. The shortened version of the NEO PI-R, containing 60 items, was completed by a subsample (109 individuals) who participated in the MAPS study but not the Mail and Phone study; facet scores could not be derived for this version. Thus, NEO PI-R data were collected from 895 participants (including 685 twins and 210 siblings of twins). Of those with NEO PI-R data, 670 had been tested for IQ as part of the MAPS study. There was no difference in mean IQ between those who completed the NEO PI-R and those who did not. A summary of the final number of participants with NEO PI-R data, according to zygosity, is shown in Table 1.

IQ Measures

IQ data were obtained from a shortened version of the Multidimensional Aptitude Battery (MAB; Jackson, 1998), which included three verbal subtests (information, arithmetic, vocabulary) and two performance subtests (spatial, object assembly). The MAB generates scores for full-scale, verbal IQ (VIQ) and performance IQ (PIQ) based on Canadian normative data. Each subtest was presented in multiple-choice format and was timed at 7 minutes. No penalties were given for guessing and twins were encouraged to answer every item in the time limit. Scoring and administration were computerized. For a full description of the IQ testing protocol see Luciano and colleagues (2003).

Statistical Analysis

Means, variances and covariances were tested for equality across birth order and zygosity to ensure that sampling was random and that groups were drawn from the same population. This assumptions testing was performed in Mx (Neale, 1997) within a maximum likelihood framework; the chi-square likelihood ratio test was used to compare the goodness-of-fit for different models. The mean effects

of sex and age were also tested within the maximum likelihood models.

The best fitting means and variance models (including covariate effects where significant) for each measure were extended to include a model for the covariance between twins based on genetic theory. For monozygotic (MZ) twins, the covariance was defined as additive genes (A) + dominance genes (D) + common environment (C), whereas for dizygotic (DZ) twins, the covariance was defined as .5A + .25D + C. Unique environmental (E) sources of variance are unshared between co-twins so only contribute to trait variance. As C and D are negatively confounded in the classical twin design, either C or D was modeled based on the size of the difference between MZ and DZ correlations (more similar MZ and DZ correlations indicate C effects). Genetic and environmental parameters were estimated by maximum likelihood in Mx, and the fit of submodels (which excluded D or C) was tested using the chi-square likelihood ratio test. Unique environment (E), which incorporates measurement error, was not excluded from the model. Significant phenotypic correlations between the extraversion facets and IQ measures were decomposed into genetic and environmental components of variance using a Cholesky (or triangular) decomposition of covariance (see Neale & Cardon, 1992).

Results

Data Cleaning

Where participants had missing data for fewer than two items for a single facet of the NEO PI-R (maximum of 3.8% for E6, positive emotions), the missing data were recoded as the mean for that item according to sex, otherwise the total facet score was coded as missing. A maximum of 11 cases for E1 (warmth) were recoded as missing, with 13 cases defined missing for the extraversion domain score. Table 2 displays the descriptive statistics for the extraversion variables. As data were collected from both

Table 3

Results of Univariate Model Fitting to Extraversion Measures: -2LL and df of the Base Model (ADE) and Change in -2LL ($\Delta\chi^2$) and df of the Nested Model (AE) and the Proportions of Variance (95% Confidence Intervals) Explained by the ADE and AE Models

	-2LL	$\Delta\chi^2$	Proportion of Variance (95% confidence intervals)		
	ADE (df)	AE (1)	A	D	E
Extraversion Domain	2453.34 (874)	4.97*	0 (0, .27) .48 (.27, .63)	.42 (.07, .56) —	.58 (.44, .76) .87 (.78, .96)
Warmth (E1)	4339.62 (770)	10.51*	0 (0, .21) .62 (.46, .74)	.54 (.21, .66) —	.46 (.34, .63) .78 (.68, .89)
Gregariousness (E2)	4614.56 (767)	.21	.14 (0, .39) .25 (.10, .39)	.13 (0, .45) —	.72 (.55, .90) .75 (.61, .90)
Assertiveness (E3)	4693.83 (772)	2.24	0 (0, .34) .23 (.07, .39)	.33 (0, .49) —	.67 (.51, .87) .77 (.61, .93)
Activity (E4)	4263.65 (772)	1.93	0 (0, .27) .14 (0, .32)	.25 (0, .45) —	.75 (.55, .98) .86 (.68, 1)
Excitement-Seeking (E5)	4397.24 (771)	1.06	0.02 (0, .39) .27 (.12, .41)	.31 (0, .48) —	.67 (.52, .85) .73 (.58, .87)
Positive Emotions (E6)	4459.17 (770)	4.42*	0 (0, .36) .60 (.45, .71)	.47 (.04, .60) —	.53 (.40, .70) .80 (.70, .89)

Note: * $p < .05$

the full and the shortened version of the NEO PI-R, a z -score was calculated for the domain score in order to combine the data. All variables were normally distributed, with the maximum number of univariate outliers excluded from analyses totalling four for E6, positive emotions. Verbal IQ scores ranged 81 to 143 (mean of 110.5 ± 11.1), while performance IQ scores ranged 68 to 151 (mean of 113.2 ± 15.8).

Assumptions Testing

Results showed that: the mean of male MZ twins was lower than that of male same-sex DZ twins for the activity facet (E4); the female mean in the two opposite-sex groups differed from each other (lower for female first-born) for the excitement-seeking facet (E5); and the variance of females was larger than males for gregariousness (E2) and excitement-seeking facets (E5). As the violations of homogeneity of means were not consistent across facets, and zygosity or birth order factors, and due to the large number of multiple tests performed, they were considered type 1 errors and were constrained equal in the subsequent genetic models. The variance differences between sexes for E2 and E5 were of greater significance than the means tests and were therefore modeled in the genetic analyses.

Females scored between one and two points higher on warmth (E1), gregariousness (E2), and positive emotions (E6) facets, and significant age effects were found for gregariousness (E2), activity (E4), excitement-seeking (E5), and positive emotions (E6) facets. Correlations between these extraversion facets with age were positive for E4 ($r = .09$) and E6 ($r = .08$), but negative for E2 ($r = -.07$) and E5 ($r = -.13$). Where significant, sex and age adjustments (covariate effects) to the means were incorporated into the genetic models. Due to the small sample size of DZ same-sex

and opposite-sex groups, sex-limited gene effects on the traits were not investigated. Twin-sibling covariances could be equated with DZ twin covariances, indicating that it was valid to treat siblings as DZ twins, notwithstanding their difference in age.

The Heritability of Extraversion

Table 2 displays the twin pair correlations for MZ and DZ (including nontwin sibling pairs) twins for each extraversion measure as estimated in Mx. For all measures, the DZ twin correlation was less than half the MZ twin correlation, suggesting that nonadditive effects of genes (D) explain more variance in extraversion than common environmental influences (C). Therefore a model containing additive genetic, nonadditive genetic and unique environmental variance (ADE) was fitted to the raw data for each measure.

Results of the univariate genetic modeling of the extraversion measures are displayed in Table 3. Nonadditive genetic influences (D) could be removed as a source of variation — without significantly reducing model fit — for gregariousness (E2), assertiveness (E3), activity (E4) and excitement-seeking (E5). A significant drop in the fit of the model was observed for the E domain, warmth (E1) and positive emotions (E6) indicating that nonadditive genetic influences were a significant source of variation for these measures.

Extraversion and IQ Relationship

Table 2 displays the phenotypic correlations between extraversion measures and VIQ and PIQ. Excitement-seeking (E5) was significantly negatively correlated with VIQ ($r = -.15$, $p < .01$) and PIQ ($r = -.11$, $p < .01$), such that introverts tended to have higher IQs. The gregariousness facet (E2) was marginally significantly

correlated with verbal IQ, such that those with lower gregariousness scored higher on verbal IQ. No other extraversion facets were correlated with either of the IQ measures. As excitement-seeking was the only facet significantly correlated with both VIQ and PIQ, the remainder of the analyses were focused on the relationship between the excitement-seeking facet (E5) and VIQ and PIQ.

Multivariate Genetic Modeling

A multivariate analysis was conducted to determine whether the phenotypic correlation between excitement-seeking (E5) and IQ (verbal and performance) was due to common genes. As univariate results indicated an absence of nonadditive genetic (D) effects on excitement-seeking, and because previous studies (e.g., Wainwright et al., 2005) have shown common environment (C) to significantly affect VIQ, a multivariate ACE model was specified. An additive genetic and unique environment (AE) model best fitted the data as indicated by the nonsignificant change in chi-square of the nested model ($\Delta\chi^2_6 = 4.49$, $p > .05$). A common and unique environment (CE) model resulted in a significant change in chi-square ($\Delta\chi^2_6 = 22.45$, $p < .001$) and was not investigated further. The reduced AE Cholesky decomposition, in which nonsignificant loadings were fixed to zero, showed the presence of three genetic factors. The standardized parameter loadings of the final model and their 95% confidence intervals are displayed in Figure 1. The first genetic factor loaded on PIQ (.71), VIQ (.55) and excitement-seeking (–.17), but was most clearly defined by PIQ. The second and third genetic factors were specific to VIQ (.56) and excitement-seeking (.41), while the unique environmental factors were largely specific to each variable with some covariation between the IQ measures. Genetic correlations of –.39 and –.27 were estimated between excitement-seeking and respective PIQ and VIQ.

Discussion

This study examined the phenotypic and genetic relationship between the facets of extraversion, verbal IQ and performance IQ. Results showed that the excitement-seeking scale (E5) was significantly correlated with both verbal and performance IQ, and consistent with our hypothesis, this correlation was negative, such that lower excitement-seeking scores were related to higher IQ scores. Gregariousness was found to negatively correlate with verbal IQ but not performance IQ. All extraversion facets were influenced by genes with no support for common environmental effects on trait variance. A decomposition of the underlying genetic and environmental covariance between extraversion and IQ showed that genes solely mediated the relationship between excitement-seeking, VIQ and PIQ.

Genetic modeling confirmed that the warmth (E1) and positive emotions (E6) scales were influenced by additive and nonadditive genes, while the gregariousness

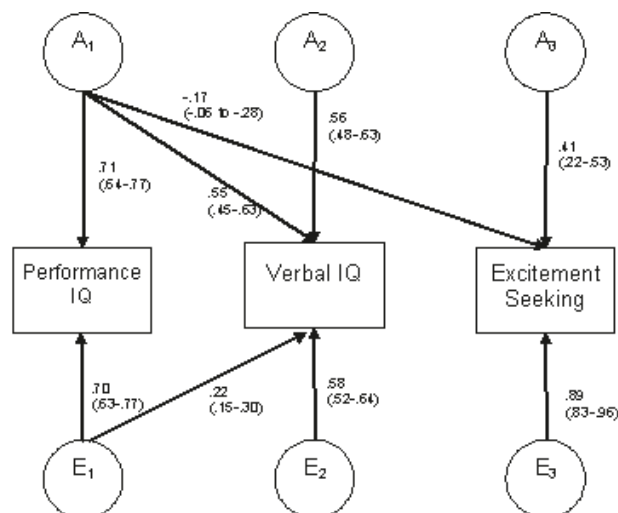


Figure 1

Standardized path coefficients for the reduced Cholesky decomposition, where A represents additive genetic factors and E represents unique environmental factors. 95% confidence intervals are shown in brackets.

(E2), assertiveness (E3), activity (E4) and excitement-seeking (E5) scales were influenced by additive genes only. The heritabilities of these facets (ranging .25 for activity to .54 for warmth) were consistent with those of Jang et al. (1996, 1998, 2002), although they found nonadditive gene effects for assertiveness and excitement-seeking in addition to warmth. In our study, the correlations of the DZ twins were less than half that of the MZ twins for all measures indicating that nonadditive genes may be an important source of variance in extraversion, although there was insufficient power to detect this in all facets. Alternatively, DZ sibling contrast effects, which have been reported by Eaves and Silberg (2005), may have accounted for the lower DZ twin correlations rather than a dominance effect. Sibling contrast effects would be such that high extraversion in one sibling lowers extraversion in the other sibling.

In agreement with some previous studies (e.g., Chamorro-Premuzic & Furnham, 2006), we observed a nonsignificant correlation between the extraversion domain score and IQ. Furthermore, excitement-seeking and gregariousness were the only extraversion facets found to be significantly correlated with IQ. These observed negative correlations were in line with previous studies reporting correlations ranging –.03 to –.07 between the extraversion domain score and measures of general ability (Austin et al., 2002; Moutafi et al., 2003). It is possible that the negative correlation previously reported for the domain score is driven primarily by the excitement-seeking facet. The gregariousness scale showed marginal significance with IQ; it may be that gregariousness and excitement-seeking show an enhanced relationship due to their common influences on risk taking behavior (e.g., Miller et al., 2004).

Multivariate genetic analysis of excitement-seeking and IQ supported a common genetic origin, with the common additive genetic factor loading on excitement-seeking (explaining 3% of variance), VIQ (30%) and PIQ (50%). Most of the genetic variance (85%) in excitement-seeking was unrelated to intelligence, and is likely to overlap with the genetic variance in the other facets of extraversion. The nonshared environmental influences on extraversion were specific to this trait, indicating that the relationship between excitement-seeking, VIQ and PIQ was due solely to additive genes. The absence of overlapping unique environmental influences on excitement-seeking and IQ suggests that directional causation models in which either excitement-seeking causes variation in IQ, or vice versa, are not appropriate explanations for the relationship since in these models the total variation (i.e., genetic and environmental) in one trait influences the variance of the other. This argues against the interpretation of the negative relationship between excitement-seeking and IQ in terms of brighter students becoming more introverted as they progress through school (Eysenck & Cookson, 1969). A physiological rather than behavioral pathway (e.g., brighter students preferring academically related pursuits, which limits the development of excitement-seeking tendencies) is likely involved.

This physiological pathway may relate to dopaminergic mechanisms which have been linked to extraversion and intelligence (de Frias et al., 2005; Pevic, 1999; Reuter & Hennig, 2005; Rammsayer, 1998). Specifically, an important role of dopamine in working memory, executive functioning and PIQ has been shown (Fossella et al., 2002; Tsai et al., 2002). Our results reflect these findings as the genetic correlation with excitement-seeking was stronger for PIQ than VIQ. Furthermore, novelty-seeking - a related phenotype of excitement-seeking - has been found to be associated with a polymorphism in the DRD4 gene (Benjamin et al., 1996; Keltikangas-Jarvinen et al., 2003; Strobel et al., 1999), although negative findings have also been reported (see Kluger et al., 2002). The functional polymorphism of the catechol O-methyltransferase (COMT) gene has also been implicated as a candidate gene for extraversion and intelligence: it is essential in the metabolic degradation of dopamine in the prefrontal cortex. In a sample of 363 males and females, those homozygous for the Val allele (presumably related to lower dopamine levels) showed significantly higher scores on the exploratory excitement subscale of novelty seeking and NEO-FFI extraversion (Reuter & Hennig, 2005). Consistent with the negative relationship observed between excitement-seeking and IQ, in a study of 292 men, carriers of the Val allele performed worse on executive functioning and visuospatial tasks than carriers of the Met/Met genotype (de Frias et al., 2005). Previous studies (Egan et al., 2001; Malhotra et al., 2002) have similarly shown that homozygous Met

allele carriers have superior prefrontal cortex and executive functioning.

The effect of individual genes on complex traits is thought to be small (explaining as little as 1% of trait variance), so while the shared variance between excitement-seeking and IQ was estimated at only 2% in our study, multivariate association analysis of these variables can increase the statistical power to detect the common gene/s influencing their variation (Lange et al., 2003). The COMT polymorphism would appear to be a good candidate to investigate for pleiotropic effects on excitement-seeking and IQ.

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