The genetic and environmental relationship between Cloninger's dimensions of temperament and character

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Abstract

The purpose of this study was to determine whether Cloninger's revised 7-factor model of personality showed incremental validity over his four dimensions of temperament. A sample of 2517 Australian twins aged over 50 between 1993 and 1995 returned completed self-reported measures of Self-directedness, Cooperativeness, and Self-transcendence from Cloninger's Temperament and Character Inventory. Many of these twins had participated in a 1988 study containing Cloninger's temperament measures of Harm Avoidance, Novelty Seeking, Reward Dependence and Persistence. Contrary to theoretical expectations, univariate analyses revealed that familial aggregation for the character dimensions could be entirely explained by additive gene action alone. Although temperament explained 26, 37 and 10% of additive genetic variance in Self-directedness, Cooperativeness and Self-transcendence, respectively, seven genetic factors were required to explain the genetic variance among the TPQ dimensions, and almost all of the non-shared environmental variance was unique to each dimension of character. Our results indicate that the inclusion of all seven dimensions in a taxonomy of personality is warranted.

Keywords

Personality; Cloninger; Temperament; Character; Genes; Twins

1. Introduction

Cloninger's theory of personality is based on a synthesis of information from family studies, studies of longitudinal development, and psychometric studies of personality structure, as well as neuropharmacologic and neuroanatomical studies of behavioral conditioning and learning in man and animals (Cloninger, 1987). His revised biosocial model of personality posits seven domains of personality as measured by the Temperament and Character Inventory (TCI) (Cloninger, 1994): four temperament (Harm Avoidance, Novelty Seeking,

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Reward Dependence and Persistence) and three character domains (Self-Directedness, Cooperativeness, and Self- Transcendence) (Cloninger, 1994).

Originally, the model included only three dimensions of temperament; Harm Avoidance, Novelty Seeking, and Reward Dependence as measured by the 100 item self-report Tri-Dimensional Personality Questionnaire (TPQ) (Cloninger, 1986). The Persistence items in Reward Dependence were later separated and recognised as a fourth, separately inherited dimension of personality (Cloninger, 1994; Stallings, Hewitt, Cloninger, Heath, & Eaves, 1996). Temperament was conceptualised as corresponding to heritable biases in memory processing involved in pre-semantic perceptual processing and encoding of concrete visuospatial structural information and affective valence. These processes were hypothesized to be functionally organized as independently varying brain systems aligned to specific monoaminergic cell bodies which in turn are responsible for autonomic responses involved in the activation, maintenance and inhibition of behaviour (such as differences in classical conditioning, operant conditioning and non-associative learning, i.e. sensitization and habituation) (Cloninger, 1994). These dimensions were intended to provide differential diagnosis within personality disorder (PD) populations, with combinations of extreme variants in the four basic dimensions corresponding to traditional PD taxonomy (Cloninger, 1987). Cloninger has subsequently argued that a major limitation of temperament profiles is that they are not diagnosis specific because variation in these continuous trait measures does not distinguish clinical from non-clinical populations. Additional aspects of personality were therefore required to enable such distinctions.

Accordingly, the model was revised (Cloninger, Svrakic, & Przybeck, 1993) to include three dimensions of character: Self-directedness, Cooperativeness and Self-transcendence. These dimensions were based on a synthesis of information about social and cognitive development and descriptions of personality development in humanistic and transpersonal psychology (Cloninger, 1994; Cloninger et al., 1993). Specifically, the scales were designed to measure conceptual memory biases involved in the processing or conversion of sensory input into abstract symbols which translate into concepts of personal, social and universal identity. Self-directedness measures individual self-acceptance, Cooperativeness measures acceptance of other people, while Self-transcendence captures the degree to which an individual feels a part of nature and the universe at large. These dimensions were derived from factor analyses of childhood personality inventories (Sigvardsson, Bohman, & Cloninger, 1987) as well as from investigation of items from the NEO Personality Inventory, Multidimensional Personality Questionnaire, Profile of Mood States, and Minnesota Multiphasic Psychological Inventory which identified additional dimensions of personality uncorrelated with Cloninger's temperament dimensions. According to the model, individuals with mature personalities are described as self-reliant, cooperative, and self-transcendent, in contrast to individuals with PD's who are troubled with self-acceptance, are intolerant or revengeful towards others and are unfulfilled (Cloninger et al., 1993).

According to Cloninger's model, perceptual memory processes relating to temperament operate independently of abstract-conceptual, intentional or declarative processes which define conceptual memories. Lesion studies involving monkeys (Bachevalier, 1990; Malamut, Saunders, & Mishkin, 1984) support a physiological distinction between

perceptual and conceptual memories since monkeys with combined amygdalo-hippocampal removal show severe deterioration in conceptual memory tasks, while their functioning on perceptual memory tasks is largely unaffected (Cloninger et al., 1993). Support for this distinction is also based upon ethologic studies examining the sequential evolution of personality dimensions wherein Cloninger argues that temperament development preceded that of character (Cloninger & Gilligan, 1987). Cloninger has stressed that the temperament and character domains, although distinct, are part of an 'iterative epigenetic process' whereby each interacts with the other in motivating behaviour (Cloninger et al., 1993).

Each of the temperament and character dimensions has demonstrated good test–retest correlations irrespective of the population sampled (see Cloninger, 1994). Internal reliabilities range from 0.65 to 0.87 for the temperament and from 0.84 to 0.89 for the character dimensions (Cloninger et al., 1993). Correlations between TPQ self-reports and interviewer ratings of personality range from 0.60 to 0.76 (Svrakic, Przybeck, Whitehead, & Cloninger, 1994). Numerous factor analytic studies have confirmed the factor structure of the temperament (Bagby, Parker, & Joffe, 1993; Sigvardsson et al., 1987; Stallings et al., 1996; Svrakic, Przybeck, & Cloninger, 1991; Waller, Lilienfeld, Tellegen, & Lykken, 1991) and character domains (Cloninger, 1994; Pelissolo & Lepine, 2000). Nevertheless, there remains debate over Persistence as a reliable dimension of temperament (Lepine, Pelissolo, Teodorescu, & Teherani, 1994; Pelissolo & Lepine, 2000). Several studies have suggested that Reward Dependence and Persistence are not as psychometrically 'robust' as the other temperaments (Brandstrom et al., 1998; Lepine et al., 1994; Pelissolo & Lepine, 2000). There does however appear to be stronger empirical evidence based on multiple regression (Nagoshi, Walter, Muntaner, & Haertzen, 1992), factor analytic (Kleifield et al., 1993; Stallings et al., 1996) and joint analytic studies (Kleifield, Sunday, Hurt, & Halmi, 1993; Stallings et al., 1996) in favor of Persistence as an independent dimension, although specific brain systems are yet to be identified.

Two large scale epidemiological twin studies designed to investigate the genetic and environmental structure of temperament (Heath, Cloninger, & Martin, 1994; Stallings et al., 1996) have also supported the four factor model at the phenotypic level, although genetically, one of the studies did not find evidence of an additive genetic factor for Persistence in adult males (Stallings et al., 1996). More recent factor analytic studies based on the full TCI (Brandstrom et al., 1998; Richter, Eisemann, & Richter, 2000) have supported Cloninger's revised seven factor model of personality (Cloninger et al., 1993), however, some factor analytic studies have suggested that the seven TCI factors can be reduced to five factors by combining high Harm Avoidance with low Self-directedness and by combining Reward Dependence with Cooperativeness (Herbst, Zonderman, McCrae, & Costa, 2000).

1.1. Objective

If the 'epigenesis' of self-concepts underpinning the dimensions of character is partly the product of social learning and emerging cultural perspectives (Cloninger & Gilligan, 1987; Cloninger et al., 1993) then character development ought to be influenced by shared environmental effects. This is in contrast to the heritable dimensions of temperament for

which familial aggregation is best explained by additive genetic effects alone (Heath, Cloninger, & Martin, 1994; Stallings et al., 1996). Previously, Kirk et al. found that additive genetic effects accounted for 48% of the variance in Self-transcendence scores for men and women alike (Kirk, Eaves, & Martin, 1999). In addition to demonstrating trait heritability, it is desirable to determine whether a trait provides additional information beyond that which can be already explained by existing personality taxonomies. To date, no other study has investigated the multivariate relationship between the dimensions of temperament and character. In addition to exploring the genetic etiology of the three dimensions of character, the central aim of this study is to determine the degree to which genetic and environment variance in Cloninger's dimensions of character can be explained by the four dimensions of temperament. More generally, we will evaluate the extent to which genetic and environmental determinants of each of the seven TCI dimensions are unique (that is, unexplained by the other factors), so as to determine whether their inclusion in a taxonomy of personality is warranted.

2. Method

2.1. Subjects

Twins were drawn from the Australian National Health and Medical Research Council Twin Register (ATR). The ATR is a volunteer register founded in 1978 with almost 28,000 twins of all types and all ages enrolled and in various stages of active contact. Analyses have shown that the ATR is typical of the Australian population in many respects including the prevalence of psychiatric symptoms (Kendler, Heath, Martin, & Eaves, 1986), although the ATR sample tends to be slightly more middle class and educated than average, particularly for males (Baker, Treloar, Reynolds, Heath, & Martin, 1996).

Data for this study were collected from two studies. In 1988, an extensive Health and Lifestyle Questionnaire (HLQ) was mailed to a community-based sample of 7614 twin individuals born before 1964 referred to as 'Cohort 1' (Jardine, Martin, & Henderson, 1984). The HLQ covered a wide range of behavioural and personality measures and included the Harm Avoidance, Novelty Seeking, Reward Dependence and Persistence scales from a shortened version of Cloninger's Tri-Dimensional Personality Questionnaire (TPQ) (Heath, Cloninger, & Martin, 1994). Between November 1993 and July 1995, 4186 twins who participated in Cohort 1, together with 376 newly appended twins, all of whom were aged 50 years or above at the time they were approached and asked to participate in a study of elderly Australian twins referred to as the 'Aged Study'. This study also covered a wide range of behavioural and personality measures which included the character scales (Self-directedness, Cooperativeness, and Self-transcendence) from the shortened version of Cloninger's Temperament and Character Inventory (TCI). The TPQ scale scores from Cohort 1 were included if the subject was eligible (i.e. over 50 years of age) to participate in the Aged Study.

In the Aged Study, complete responses were received from 3040 individuals, comprising 1224 complete pairs and 574 singles. Having excluded deaths and non-contacts, the complete pair and individual response rates were 61 and 69% respectively. The average age of these respondents was 61.9 years ± 8.9. In both waves, zygosity of twins was diagnosed

by response to two standard items (Martin & Martin, 1975), supplemented in ambiguous cases by examination of photographs supplied by the respondents. Such procedures have previously demonstrated at least 95% agreement with diagnoses based on extensive blood sampling (Martin, 1975; Ooki, Yamada, Asaka, & Hayakawa, 1990).

In order to assess the test–retest reliability of the temperament scales in the 1988 questionnaire, a repeat questionnaire was mailed out to the first 1000 twins (500 male and 500 female) who returned completed response booklets. Complete retest questionnaires were received from 407 male and 426 female respondents. Since these twins were surveyed before all of the original survey responses had been returned in 1988, uncooperative twins were therefore under-sampled. The average test–retest period was 2.1 years.

2.2. Measures

The 1988 survey included an abbreviated 54-item version of Cloninger's Tri-dimensional Personality Questionnaire (TPQ) (Cloninger, Przybeck, & Svrakic, 1991) designed to assess three higher order dimensions of temperament: Harm Avoidance (HA) (18 items); Novelty Seeking (NS) (18 items); Reward Dependence (RD) (14 items), and Persistence (PERS) (4 items). The TPQ was scored on a three-point [Yes/Don't know/No] with "Don't know" responses recorded as missing. The Aged Study questionnaire contained an abbreviated 35-item version of the character scales from Cloninger's Temperament and Character Inventory (TCI) (Cloninger et al., 1991): Self-directedness (DIRECT) (10 items); Cooperativeness (COOP) (10 items); and Self-transcendence (TRANS) (15 Items). The character items were also measured on a three-point scale [No/Don't know/Yes] with "Don't know" responses recorded as missing.

2.3. Statistical analysis

Prior to calculating raw cumulative scores for all seven dimensions, the imputation option of PRELIS 2.20 (Jöreskog & Sörbom, 1998) was used to impute missing values using sex and the full number of items within each dimension as matching variables. For more details on this method see Gillespie, Johnstone, Boyce, Heath, and Martin (2001). Imputation results for the temperament dimensions based on the entire Cohort 1 sample are described elsewhere (Gillespie et al., 2001). Temperament data for each subject was included in the analyses if the subject was eligible to participate in the Aged Study. Although less than 1% of the total number of character items in each scale were imputed, imputation of missing items increased the total number of subjects with complete responses for the Self-directedness, Cooperativeness and Self-transcendence scales by 3% (*N*=2743), 2% (*N*=2727) and 6% (*N*=2738) respectively. Exactly 2517 subjects returned complete data on all three character dimensions.

2.4. Analysis of raw ordinal data

In order to make use of complete and incomplete data observations we conducted Maximum Likelihood analyses of raw ordinal data using Mx (Neale, 1999) which permitted us to test hypotheses concerning (i) the equality of response distributions within twin pairs, across sex and zygosity and (ii) the equality and causes of correlations. Data were analyzed under a multivariate normal liability threshold model (i.e. the same assumptions used in the

estimation of polychoric correlations in Prelis (Jöreskog & Sörbom, 1993), with estimation of genetic and environmental parameters and threshold values. Combining complete and incomplete twin pairs has the advantage of increasing the accuracy when estimating thresholds, thereby improving estimation of the polychoric correlations. Preliminary analyses revealed that the optimum number of ordinal categories for the temperament and character dimensions was five and six, respectively, which balanced the need for minimal information loss and greater computational efficiency. This resulted in no significant change in either the point estimates of the polychoric correlations or their variances.

2.5. Genetic analysis

Standard biometrical genetic model fitting methods were used (Neale & Cardon, 1992) which decompose the total variance in an observed trait into additive (A) and non-additive (D) (dominance or epistasis) genetic variance as well as shared (C) and unique (E) environmental variance. MZ cotwins are genetically identical so correlations for additive and non-additive genetic effects between MZ twins are both 1.0. For DZ twins, the correlations for additive and non-additive genetic effects are 0.5 and 0.25, respectively. An important assumption of the biometrical model is that shared environmental effects correlate to an equal extent in MZ and DZ twin pairs (Kendler, Neale, Kessler, Heath, & Eaves, 1994; Xian et al., 2000). Non-shared environmental effects are by definition uncorrelated and also reflect measurement error including short-term fluctuations.

In the absence of data from separated twin pairs, half siblings, or similar pairs of relatives, non-additive and shared environmental effects are confounded, so that only one can appear in a given model. Non-additive effects reduce the DZ correlation to less than one-half the corresponding MZ correlation, while shared environmental effects increase the DZ correlation above one half the MZ correlation. Since additive genetic effects are generally expected to be small, we compared the fit of the full ACE model, and models dropping either additive genetic parameters (CE model) or shared environmental parameters (AE model) by likelihood-ratio-chi-square test (Neale & Cardon, 1992). Detecting dominance is unlikely given the large sample sizes required (Martin, Eaves, Kearsay, & Davies, 1978), and since it is inconceivable for complex behavioural traits to be measured without error, all models include an estimate of E.

Both univariate and multivariate models based on Maximum Likelihood analysis are initially fitted separately for males and females, and then jointly to all four same-sex groups. Adding the separate log-likelihood values for males and females and then subtracting this value from the log-likelihood of the joint fit to males and females (Jardine & Martin, 1984) permits us to determine whether the structure and sources of variance are qualitatively and quantitatively equivalent across sex.

2.6. Multivariate analyses

Multivariate analysis makes use of the additional information in the cross-correlations between relatives for different traits and permits us to determine the extent to which genetic and environmental influences are shared in common by several traits or are trait specific (Heath, Cloninger, & Martin, 1994). Since our central aim was to determine the proportion

of variance in the character scales which could be explained by temperament we fitted multivariate triangular Cholesky decomposition models to the data. The Cholesky is a method of triangular decomposition where the first variable is assumed to be caused by a latent factor that can also explain some or all of the variance in the remaining variables; the second, independent factor is assumed to be influenced by an additional latent factor that can explain variance in the second as well as remaining variables; and this pattern continues until the final observed variable is explained by a latent variable, which is uncorrelated with all preceding factors and influences only one variable (i.e. a factor specific to one variable). The same factor structure is repeated for each source of variance (A, C, and E). We conducted multivariate analyses using Mx, and compared model fits in the same way as in the univariate analyses.

In order to determine the extent to which the character dimensions assessed new dimensions of genetic and environmental variance, we entered the four temperament dimensions (HA, NS, RD and PERS) followed by three character dimensions (DIRECT, COOP and TRANS). We then repeated the analyses but reordered the variables to predict the proportion of variance in the four temperaments which could then be explained by latent genetic and environmental effects underlying the character dimensions. A seven-factor Cholesky solution proved too computationally demanding for raw ordinal data analysis. Since comparisons between the raw ordinal and continuous data methods based on the univariate, three and four factor multivariate models all yielded highly comparable results, we therefore analysed the raw continuous data in Mx after transferring the raw categories to normal weights in order to minimize skewness as well as improve computational efficiency.

3. Results

The number of complete twin and incomplete twin pair responses for each scale after imputation, together with measures of internal consistency (Cronbach α) appear in Table 1.

3.1. Tests of threshold homogeneity

The number of significant differences in the threshold distributions within twin pairs and across zygosity was no greater than expected by chance. There were significant sex differences in the response distributions for Harm Avoidance, Novelty Seeking, Reward Dependence, Self-directedness and Cooperativeness but none for Persistence or Self-transcendence. Females had significantly lower scores on Harm Avoidance, Reward Dependence, Novelty Seeking and Cooperativeness scores but higher scores on Self-directedness.

3.2. Polychoric correlations

Phenotypic polychoric correlations between the seven dimensions of personality (ignoring the twin nature of the data) for males and females appear in Table 2. For males, there was a moderate correlation between Harm Avoidance and Self-directedness (−0.40), a moderate correlation between Reward Dependence and Cooperativeness (0.33), as well between Reward Dependence and Self-transcendence (0.21). There was also a small correlation between Persistence and Self-transcendence (0.18). This pattern was fairly similar for

female twins except that the correlations between Reward Dependence and Cooperativeness (0.23), and between Reward Dependence and Self-transcendence (0.11) were smaller. Correlations between the dimensions of character were small to moderate; the highest was between Cooperativeness and Self-transcendence (0.29) for male and female twins alike. Correlations between the dimensions of temperament were also small to moderate. The male and female correlations between Novelty Seeking and Reward Dependence were similar (0.30 versus 0.28), while the correlation between Harm Avoidance and Novelty Seeking was higher for males (−0.30 versus −0.21).

3.3. Twin pair correlations

Maximum Likelihood twin pair polychoric correlations and 95% confidence intervals for the temperament and character dimensions appear in Table 3. All of the DZ correlations for the dimensions of temperament and character were less than their MZ counterparts suggesting genetic effects. We therefore proceeded to correlation contrasts and univariate modeling in order to formally test hypotheses concerning the sources of familial aggregation in each of the dimensions.

3.4. Correlation contrasts

A model which fixed all MZ and DZ correlations to zero gave a very poor fit ($P<0.001$, by likelihood-ratio-chi-square test) indicating significant twin pair resemblance for every variable. Likewise, a model which fixed MZ and DZ correlations equal gave a poor fit [Harm Avoidance (-2LL=27.57, d.f.=4, $P<0.001$), Novelty Seeking (-2LL=17.59, d.f.=4, $P<0.001$), Reward Dependence (-2LL=15.11, d.f.=4, $P<0.001$), Persistence (-2LL=17.09, d.f.=4, $P<0.01$), Self-directedness (-2LL=9.65, d.f.=4, $P<0.05$), Cooperativeness (-2LL=14.67, d.f.=4, $P<0.01$), and Self-transcendence (-2LL=13.30, d.f.=4, $P<0.05$)] suggesting that the significant twin pair resemblance was likely due to genetic rather than shared environmental effects. Finally, a model which equated the same and opposite sex DZ twin pair correlations fitted the data well [Harm Avoidance (-2LL=5.98, d.f.=3, $P=0.11$), Novelty Seeking (- 2LL=2.63, d.f.=3, $P=0.45$), Reward Dependence (-2LL=1.01, d.f.=3, $P=0.80$), and Persistence (-2LL=3.47, d.f.=3, $P=0.33$), Self-directedness (-2LL=1.81, d.f.=3, $P=0.61$), Cooperativeness (-2LL=2.26, d.f.=3, $P=0.52$), and Self-transcendence (- 2LL=1.07, d.f.=3, $P=0.78$)] suggesting that sex-dependent genetic effects were unlikely to be present.

3.5. Univariate analysis

In the analysis of same-sex pairs, we found no evidence of significant sex differences in either the saturated or nested models on any of the seven personality dimensions, so we extended our univariate analyses to include data from opposite sex DZ twin pairs with separate thresholds for sex. We then combined all the data into a two group model (MZ and DZ twins) which allowed for age and sex effects in response frequencies (i.e. threshold values) and obtained identical results. The best fitting univariate model for each of the seven dimensions included additive genetic and non-shared environment effects. Standardised estimates of the additive genetic and non-shared environmental parameters are shown in

Table 4. Additive genetic effects explained 30 to 41% of the total variance in the dimensions of temperament and 27 to 44% of the variance in character.

3.6. Multivariate analysis

When we fitted multivariate genetic triangular decomposition models to the four temperament and three character dimensions no significant sex differences in either the saturated or nested models were found and so our analyses were extended to include data from opposite sex DZ twin pairs with separate thresholds for sex. As in the univariate case we then combined all the data into a two group model (MZ and DZ twins) which allowed for age and sex effects in response frequencies (i.e. threshold values) and obtained identical results.

In the multivariate analysis of the four temperaments, both the CE (-2LL=51.86, d.f.=10, *P*<0.001) and E (-2LL=184.18, d.f.=20, *P*<0.001) models gave a poorer fit to the data when compared to the saturated ACE (−2LL=17788.43, d.f.=6345) model, while the AE (-2LL=0.00, d.f.=10) model provided the most parsimonious fit to the data.

The multivariate analyses of the three dimensions of character also revealed that both the CE (-2LL=26.45, d.f.=6 *P*<0.001) and E (-2LL=229.98, d.f.=12, *P*<0.001) models provided a poorer fit to the data when compared to the ACE (−2LL=25951.62, d.f.=8172) model, while an AE (-2LL=0.01, d.f.=6) model provided the most parsimonious fit to the data.

We then jointly analysed the combined temperament and character dimensions, however Mx was unable to arrive at an optimal solution when a fully saturated ACE Cholesky was fitted to the data. When predicting the character from temperament an AE (−2LL=43462.63, d.f.=14515) model provided a better fit when compared to the CE (−2LL=43543.40, d.f.=14515) and E (−2LL=43885.65, d.f.=14543) models. When predicting temperament from character, the model fits were identical; the AE model provided a better fit to the data compared to the CE and E models.

As shown in Table 5, heritability estimates, derived from the multivariate analyses for the three characters ranged from 27 to 45%. Temperament explained 26, 37 and 10% of the variance in Self-directedness, Cooperativeness, and Self-transcendence respectively. Thiry-three percent (33%) of the total genetic variance in Self-transcendence was also explained by the other two dimensions of character. In terms of the non-shared environmental latent effects, most of the variance in each dimension of character was variable specific with no more than 8% being explained by either temperament or other dimensions of character.

When predicting temperament from character, multivariate heritability estimates for temperament were also moderate and ranged from 30 to 42%. Character explained 30, 11, 15 and 23% of the total genetic variance in Harm Avoidance, Novelty Seeking, Reward Dependence and Persistence respectively. With the exception of Reward Dependence (28%), only a relatively small proportion of the genetic variance within the four temperament dimensions could be explained by other dimensions of temperament. Non-

shared environmental variance was also mostly variable specific with no more than 9% being predicted by character or other dimensions of temperament.

As shown in Table 6, there was a moderate genetic correlation between Self-directedness and Cooperativeness (0.35) as well as between Cooperativeness and Self-transcendence (0.38). A moderate non-shared environmental correlation was also observed between Cooperativeness and Self-transcendence (0.25). Correlations between the genetic factors underpinning temperament ranged from small to moderate, the one exception being between Novelty Seeking and Reward Dependence (0.42). The additive genetic correlations between the temperament and character factors were small to strong: a strong additive genetic correlation (−0.50) between Harm Avoidance and Self-directedness; a small to moderate negative (−0.19) between Novelty Seeking and Cooperativeness; a moderate (0.39) correlation between Reward Dependence and Cooperativeness; as well as a moderate correlation (0.26) between Persistence and Self-transcendence. As expected, the non-shared environmental factor correlations between temperament and character were lower and the highest was between Harm Avoidance and Self-directedness (−0.26).

4. Discussion

4.1. Univariate

Given that the dimensions of character were hypothesized to be partly due to socio-cultural learning (Cloninger, 1994) we therefore expected shared environmental effects to account for a significant proportion character variance. Contrary to this expectation, we found that additive genetic effects alone provided the most parsimonious explanation for the source of familial aggregation in each dimension, and based on univariate analysis, explained 27–44% of the variance in the three characters. It is important to note that in order to reject with greater confidence either the ACE or CE models in favor of an AE model using the classical twin design of MZ and DZ twins reared together, more power (increased sample size) is required than is presently available (Martin & Eaves, 1977). Despite this limitation, our results are consistent with previous studies investigating the genetic etiology of Cloninger's dimensions of temperament (Heath, Madden, Cloninger, & Martin, 1994; Stallings et al., 1996) which found that additive genetic effects alone best explained the sources of familial aggregation accounting for 30–41% of the total variance.

4.2. Multivariate

A modest proportion of the genetic variance in Reward Dependence was explained by Novelty Seeking and Harm Avoidance. Small to modest proportions (11–30%) of genetic variance in the four temperaments could also be explained by genetic factors underpinning character. In terms of the total phenotypic variance, the contribution of character equated to no more than 18, 6, 9 and 10% of the total variance in Harm Avoidance, Novelty Seeking, Reward Dependence and Persistence respectively. Despite the overlap, the residual genetic and environmental variance components were large which suggests that the dimensions of temperament are largely independent and that the inclusion of a fourth genetic factor for Persistence is also warranted.

Although there were moderate genetic and non-shared environmental latent factor correlations, the covariance between the dimensions of character was small. Less than 2% of the total phenotypic variance in Cooperativeness was explained by latent genetic and environmental factors underlying Self-directedness. A moderate proportion of the genetic variance in Self-transcendence (33%) was explained by Self-directedness and Cooperativeness, but in terms of the total phenotypic variance, Self-directedness and Cooperativeness contributed to no more than 17% of the variance in Self-transcendence. Temperament also explained small to moderate proportions of genetic variance in the dimensions of character but in terms of the total phenotypic variance this equated to no more than 15, 15 and 8% of Self-directedness, Cooperativeness and Self-transcendence, respectively. The large genetic and environmental residuals for each dimension of character suggest that they provide additional information above and beyond the contribution of temperament.

The distinction between temperament and character follows a long tradition in psychology and neuroscience that distinguishes between behavioural conditioning of skills and habits versus higher cognitive processes. The content of the temperament dimensions was constructed to measure individual differences in behavioral conditioning whereas the content of the character dimensions was constructed to measure individual differences in rational goals and values involving propositional learning (Cloninger et al., 1993 et seq). Procedural learning of habits involves incremental learning from repetition of stimulus– response sequences, whereas propositional learning depends on observation in a single exposure. For example, persistence measures individual differences related to the partial reinforcement extinction effect in animals, whereas Self-directedness measures self-concepts related to a person's awareness of the purpose and direction of their life goals. It is well-established that procedural learning (i.e. data-driven learning of habits and skills) and propositional learning (i.e. concept-driven learning of goals and values) can be dissociated in the central nervous system (Roediger, Rajaram, & Srinivas, 1990; Zola-Morgan & Squire, 1990). Although both behavioural conditioning and conceptual learning may be equally heritable, they likely involve different brain systems evolving in different stages of the evolution of learning in animals. For example, P300 evoked responses are correlated with Self-directedness but not with any temperament dimension (Vedeniapin, Anokhin, Sirevaag, & Cloninger, 2001). Temperament and character may not differ greatly in heritability, the distinction remains important to relate personality measures to important distinctions in learning and brain systems.

A potential limitation concerns the fact that character scores were ascertained approximately five years after the temperament data was obtained. Depending on the length of the scale, test– retest reliability coefficients ordinarily exceed 0.70 for the temperament dimensions over 3- and 6- month intervals (Cloninger, 1994). The combined male and female test–retest correlations for the temperament dimensions ranged from 0.68 to 0.82 over an average period of 2.1 years. Once we included the retest correlations averaged across sex into our univariate models, additive genetic effect estimates explained 48, 49, 47 and 40% of the total phenotypic variance in Harm Avoidance, Novelty Seeking, Reward Dependence and Persistence, respectively. Retest data was unavailable for the character dimensions and

although it appears that their inclusion contributes new genetic information, further investigation based on the full version of the TCI is warranted.

Cloninger has argued that models of personality will inevitably fail if they (1) do not distinguish perceptual/conceptual aspects of memory and (2) are based solely on factor analysis of behaviour without considering the underlying biological and social determinants. Our study has explored the genetic etiology of Cloninger's dimensions of temperament and character. Contrary to theoretical expectations, familial aggregation for the three dimensions of character was entirely explained by additive genetic effects with no evidence to support the role of shared environment. Covariation between the individual character scales and the four dimensions of temperament was best explained by additive genetic and non-shared environmental effects, while moderate proportions of the additive genetic variance, particularly within Self-directedness and Cooperativeness, were explained by temperament. Nevertheless, from 57 to 82% of the genetic variance in each dimension was unique, indicating that the inclusion of all seven dimensions in a taxonomy of personality is warranted.

Acknowledgements

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Table 1

Complete and incomplete twin-pair response rates after imputation of missing values together with Cronbach alphas and 2-year test–retest correlations

	Number of twin pairs		Cronbach alphas		Test–retest correlations	
	Complete	Incomplete	Males	Females	Males	Females
Harm Avoidance	699	201	0.83	0.83	0.80	0.85
Novelty Seeking	693	206	0.69	0.69	0.75	0.74
Reward Dependence	697	204	0.58	0.60	0.65	0.65
Persistence	697	204	0.61	0.54	0.68	0.69
Self-directedness	1024	695	0.63	0.66	–	–
Cooperativeness	1024	679	0.55	0.44	–	–
Self-transcendence	1027	684	0.82	0.85	–	–

Table 2

Maximum likelihood phenotypic polychoric correlations between the dimensions of temperament and character for male (above diagonal) and female (below diagonal) twins

	1.	2.	3.	4.	5.	6.	7.
1. Harm Avoidance		−0.30	−0.15	−0.17	−0.40	−0.11	−0.22
2. Novelty Seeking	−0.21		0.30	0.01	0.00	−0.03	0.12
3. Reward Dependence	−0.17	0.28		−0.03	0.07	0.33	0.21
4. Persistence	−0.08	0.04	0.06		0.10	0.08	0.18
5. Self-directedness	−0.32	−0.03	0.08	0.00		0.21	−0.05
6. Cooperativeness	−0.17	−0.03	0.23	0.08	0.16		0.29
7. Self-transcendence	−0.14	0.12	0.11	0.17	−0.04	0.29	

Table 3

Maximum likelihood twin pair polychoric correlations with 95% confidence intervals for the dimensions of temperament and character

	Harm Avoidance		Novelty Seeking		Reward Dependence		Persistence		Self-directedness		Cooperativeness		Self-transcendence	
	r	95% C.I.	r	95% C.I.	r	95% C.I.	r	95% C.I.	r	95% C.I.	r	95% C.I.	r	95% C.I.
MZFF	0.47	0.37–0.56	0.44	0.33–0.53	0.37	0.25–0.48	0.38	0.27–0.49	0.33	0.24–0.42	0.33	0.23–0.42	0.44	0.36–0.52
MZMM	0.37	0.15–0.55	0.30	0.04–0.51	0.47	0.27–0.63	0.22	−0.02–0.43	0.42	0.24–0.56	0.22	0.03–0.39	0.42	0.24–0.57
DZFF	0.21	0.04–0.36	0.04	−0.14–0.22	0.13	−0.06–0.31	0.00	−0.18–0.18	0.19	0.05–0.32	0.13	−0.02–0.27	0.22	0.08–0.34
DZMM	−0.22	−0.53–0.18	0.26	−0.05–0.51	−0.04	−0.37–0.31	−0.18	−0.47–0.17	0.06	−0.18–0.30	0.09	−0.18–0.34	0.16	−0.09–0.39
DZFM	−0.01	−0.19–0.17	0.15	−0.03–0.31	0.02	−0.15–0.18	0.12	−0.06–0.29	0.20	0.04–0.35	−0.03	−0.18–0.11	0.29	0.14–0.42

MZFF=monozygotic female twin pairs, MZMM=monozygotic male twin pairs, DZFF=dizygotic female twin pairs, DZMM=dizygotic male twin pairs, DZFM=opposite sex dizygotic twin pairs.

Table 4

Best fitting univariate models with standardized proportions of variance for the dimensions of temperament and character

	A	C	E	−2LL	df
Harm Avoidance	0.41	–	0.59	4794.89	1592
Novelty Seeking	0.39	–	0.61	4594.57	1586
Reward Dependence	0.35	–	0.65	4017.76	1591
Persistence	0.30	–	0.70	4587.98	1591
Self-directedness	0.35	–	0.65	8600.37	2735
Cooperativeness	0.27	–	0.73	8823.17	2719
Self-transcendence	0.44	–	0.56	8808.68	2730

Table 5

Proportion (%) of additive genetic variance and non-shared environmental variance within each dimensions of character (temperament) attributable to latent effects underlying (i) temperament (character), (ii) other character (temperament) dimensions, and (iii) variance unique to each dimension

	DIRECT	COOP	TRANS		HA	NS	RD	PERS
Total genetic effects	34	27	45	Total genetic effects	42	39	35	30
%Explained by temperament	26	37	10	%Explained by character	30	11	15	23
%Explained by character	–	5	33	%Explained by temperament	–	7	28	1
%Unique variance	74	59	57	%Unique variance	70	82	57	76
Total non-shared environmental effects	66	73	55	Total non-shared environmental effects	58	61	65	70
%Explained by temperament	8	7	6	%Explained by temperament	9	2	5	4
%Explained by character	–	0	4	%Explained by character	–	5	4	1
%Unique variance	92	92	90	%Unique variance	91	93	91	95

Table 6

Additive genetic (above diagonal) and non-shared environmental (below diagonal) latent factor correlations between the dimensions of temperament and character based on a two group (MZ and DZ) model

	1.	2.	3.	4.	5.	6.	7.
1. Harm Avoidance		−0.27	−0.25	−0.13	−0.50	−0.24	−0.17
2. Novelty Seeking	−0.22		0.42	0.08	0.02	−0.19	0.13
3. Reward Dependence	−0.12	0.21		−0.08	0.12	0.39	0.13
4. Persistence	−0.09	−0.01	0.08		0.09	−0.19	0.26
5. Self-directedness	−0.26	−0.06	0.05	0.00		0.35	−0.08
6. Cooperativeness	−0.12	0.05	0.20	0.18	0.10		0.38
7. Self-transcendence	−0.15	0.14	0.15	0.14	−0.01	0.25	