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RESEARCH ARTICLE

Behavioral–genetic associations in the Human Connectome Project

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Abstract
The Human Connectome Project (HCP) provides a rich dataset of quantitative and domain-specific behavioral measures from twins and extensive family structures. This makes the dataset a unique and a valuable resource to investigate heritability and determine individual differences. Using a set of measures of behavioral domains (motor, emotion, personality, sensory, and cognition), we estimated the intraclass correlations (ICCs) and heritability of 56 behavioral measures for 4 genetically identified groups of participants: monozygotic (MZ) twins, dizygotic (DZ) twins, non-twin siblings (SB), and unrelated individuals (NR). The ICCs range varied among behavioral domains but systematically so among the four genetic groups. We found the same rank order of ICCs, from the highest values for MZ twins, statistically significantly smaller for the DZ twins and sibling group (compared to MZ), and close to zero for NR. The mean heritability values of the five behavioral domains were: cognition $h^2 = 0.405$, emotion $h^2 = 0.316$, motor $h^2 = 0.138$, personality $h^2 = 0.444$, and sensory $h^2 = 0.193$. These domains share overlapping brain networks. The heritability of motor domain was significantly smaller than cognitive, personality, and emotion domains. These findings provide new insight into the effect of genetics on the various diverse behavioral measures.

Keywords Twins · Non-twin siblings · Heritability · Behavioral domains

Introduction

The relationship between genetics, behavior and heritability is a topic of research across many different disciplines, including sociology, education, neuroscience, and politics (Toga and Thompson 2005). Behavioral genetic research studies the origin of human behavior and aims to understand the origin of individual differences and the contribution of genetic and environmental influences on individual differences (Plomin 1990). A review of the literature reveals that different traits are heritable across different domains, to varying degrees (Johnson 2011; Turkheimer 2000). A meta-analysis of twin studies published over the past 50 years (1958–2012) studied the heritability of a wide range of human traits in more than 14 million twin pairs across 39 different countries. It was found that all traits had a weighted heritability greater than zero, indicating that all human traits are heritable (Polderman et al. 2015). The study also found that twin correlations were consistent with the additive genetic variation model for the majority (69%) of the traits. This pattern of twin correlation was consistent for traits in the neurological, ear, nose and throat, cardiovascular, and ophthalmological domains. When the traits were grouped into 28 general domains, 3 of the 28 general trait domains (activities, reproduction, and dermatological) were inconsistent with the additive model, while 25 of the 28 general domains were consistent. This suggests that for many of the complex behavioral traits genetic variants can be distinguished using an additive (in the narrow sense) genetic model.

The Human Connectome Project (HCP), www.humanconnectome.org a blueprint of NIH—funded project led

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by Washington University, University of Minnesota, and University of Oxford aimed to provide state-of-the-art data. Their young adult project provides a rich dataset with questionnaire- and task-based measures that assess many different behavioral domains (Van Essen et al. 2013). These extensive behavioral measures have been studied for a large family structure of 1200 subjects. We used this source to study heritability of a comprehensive set of behavioral measures, focused on five behavioral domains: motor, emotion, personality, sensory, and cognition. We give below a short overview of the genetics studies of each domain.

Motor

Although motor skills such as walking, dexterity, strength, and endurance can be learned by practicing, some individuals can improve quicker than others, which suggests the influence of a genetic component. Missitzi et al. (2013) compared differences in monozygotic (MZ) and dizygotic (DZ) twins to elucidate the relative contribution of genes and environment on individual differences in motor control and learning. The study found that for motor control, the intrapair correlation for MZ and DZ twins were 0.77 and 0.39, respectively; heritability was estimated to be 0.68. For motor learning, the study found intrapair correlations to be 0.58 and 0.19 for MZ and DZ twins, respectively, and heritability to be 0.70. These findings suggest that heredity plays a major part in individual differences in motor control and motor learning, making them strongly genetically dependent. An earlier study of motor ability by Reed et al. (1991) measured the grip strength of twins. Correlation of grip strength of MZ twins was 0.62, while for DZ twins, it was 0.39. More genetically similar MZ twins showed a higher concordance rate with grip than DZ twins; heritability was estimated to be 0.47. Finally, a systematic review and meta-analysis (Zempo et al. 2017) found that the heritability estimates of muscle strength-related phenotypes varied widely. The mean value of heritability was 0.52. For the endurance test performance, the heritability estimate was 0.53 according to Zempo et al. (2019).

Emotion

Emotion is essential to human behavior and central to the everyday human experience because emotional traits refer to qualities such as psychological well-being, social relationships, stress, and efficacy responses (Bevilacqua and Goldman 2011; Dolan 2002). One topic of interest is how different domains interact with, and influence, each other. For example, emotion exerts a powerful influence on cognition, which encompasses qualities attention, memory, and reasoning (Dolan 2002). Another area of interest is mental disorders where emotional disequilibrium is a common denominator (Bevilacqua and Goldman 2011). With respect to heritability, emotion is moderately heritable (40–60%) (Bouchard and Loehlin 2001; Bouchard and McGue 1990) but is also influenced by environment.

Self-control inhibits undesirable behaviors and impulses, promotes desirable behaviors when faced with challenging temptations, and is very important for physical and mental wellbeing of the individuals. It has been found that (a) individuals with high self-control have more successful and fulfilling lives compared to those with low self-control, and (b) the trait of self-control relates to a wide range of behavior (de Ridder et al. 2012; Vazsonyi et al. 2017). A recent quantitative review of 31 studies based on more than 30,000 twins revealed that self-control correlation between MZ twins was 0.58, correlation for DZ twins was 0.28, and heritability was 60% (Willems et al. 2019).

An important human social behavior is communication. To recognize facial emotion during conversation is a valuable aspect of social interactions. A study of contribution of genetic and environmental factors to face-emotion recognition demonstrated a large additive genetic contribution of 75% of a common emotion recognition ability (Lau et al. 2009). For the ability to recognize specific emotions, Rappaport et al. (2018) obtained the following additive genetic values: for anger 0.4, for happiness 0.57, for sadness 0.34, for fear 0.44, for surprise 0.49, and for disgust 0.41.

Social behavior–social relationships are important for humans, and it has been shown that social-relational exposures and well-being overlap (Mann et al. 2019). In addition, if the actual social connectedness is not at the level of the person's desire, this can lead to emotional state loneliness. Research of the genetic underpinnings of loneliness found no direct contribution of genes but the dynamic interplay of the environmental factors and genes that contribute to it.

Personality

Human personality is characterized as inborn traits that influence behavior across many situations. Personality can be measured by many factors, and one way of scientifically determining personality is the five factor model (FFM) also called Big Five of personality traits described as follows: 1. Openness: appreciation for a variety of experiences. 2. Conscientiousness: planning rather than being spontaneous. 3. Extraversion: being sociable, energetic, and talkative. 4. Agreeableness: being kind, sympathetic, and happy to help. 5. Neuroticism: inclined to worry or be vulnerable or temperamental.

The human personality was described with an excellent reliability and validity by the five factor model (McCrae and Costa 1997, 2004). Importance of personality FFM leads to a research to understand biological bases of heritability of these traits. The progress was achieved to find multiple

genome-wide significant variants of FFM traits (Sanchez-Roige et al. 2018). Jang et al. (1996) studied 123 pairs of MZ twins and 127 pairs of DZ twins and determined personality using the FFM personality traits. Their results showed genetic influence on the five dimensions: neuroticism 0.41, extraversion 0.53, openness 0.61, agreeableness 0.41, and conscientiousness 0.44. Another study by Power and Pluess (2015) found that the Big Five personality traits have substantially heritable components explaining 40–60% of the variance, although identification of associated genetic variants has remained unclear.

The massive meta-analysis of Vukasovic and Bratko (2015) summarized 62 behavioral genetic studies representing more than 100,000 participants, from 4 continents and 12 countries. This meta-analysis showed, on average, personality heritability estimates of 0.39, [95% confident interval (0.35, 0.43)] which means that 39% of individual differences in personality are due to genetics. Additionally, they found following genetic influence on the FFM: neuroticism 0.37, extraversion 0.36, openness 0.41, agreeableness 0.35, and conscientiousness 0.31.

Sensory

Sensory systems such as vision, hearing, touch, taste, and smell help the brain perceive and interpret the physical world around us and react to altering circumstances. In children, difficulty in processing and integrating information can overwhelm them and create confusing behavior. However, genetic and environmental factors that contribute to individual differences in proprioception are largely unknown. One example of a sensory system is pain. The prevalence of chronic wide spread pain in the general population is 10–15% (Mansfield et al. 2016). The heritability estimate for pain was found to be 37% (Trost et al. 2015), 54% (Kato et al. 2006), and 58% according to Burri et al. (2015). In the sample of 961 female participants including 190 MZ pairs and 107 DZ pairs and 367 without co-twin participants Burri et al. (2018) found heritability of chronic pain 63% at baseline and 55% 12 years later. Authors showed the same genetic influences over time, but they found the same non-shared environmental factors influencing the pain management.

It is known that genetic differences in taste preferences may impact eating behavior and nutritional intake that consequently may effect individual's health. In a comprehensive review Chamoun et al. (2018), associated genetic variation in taste receptors with the dietary intake and health outcome. Understanding of taste biology and genetics may lead to personalized approach to dietary habits, reducing the consumption of unhealthy food with increasing the intake of healthy food. These healthy diets may help prevent obesity and consequently other chronic diseases like cardiovascular diseases, type 2 diabetes, and metabolic syndrome.

Cognition

Cognitive functions such as thinking, reading, learning, memory, reason, and attention are skills that are used to carry out simple and complex tasks. Cognitive skills take incoming information and convert it into useful knowledge on a daily basis. For example, answering the telephone involves recognition (knowing what a telephone is and what it is used for), perception (hearing the ring tone), decision-making (answering or not to answer), motor skill (lifting the phone and pushing buttons), language skills (talking and understanding language), and social skills (interacting with another human being) (Michelon 2006). Cognition traits are important in research because they are one of the most reliable behavioral traits (Haworth et al. 2010). Another reason that cognition traits are important is because they can be used to predict important social outcomes such as educational and occupational levels better than other behavioral traits (Haworth et al. 2010). The heritability of cognitive skills increases from childhood to adulthood (Briley and Tucker-Drob 2013; Haworth et al. 2010). Haworth et al. (2010) looked at data from 6 studies containing information from 11,000 twin pairs from 4 countries and found that heritability increased from 41% at adolescence to 66% at young adulthood. For one aspect of spatial cognition, the meta-analysis study of King et al. (2019) found that the spatial ability is largely heritable (0.61) and even higher for adult group of participants (0.69).

Education generally and particularly reading comprehension has been linked to economic growth in the US and internationally (UNESCO 2009 National Center for Education Statistics 2013; Hanushek and Woessmann 2012). Reading comprehension ability has a large on average heritability magnitude of 0.59 with a small yet significant average shared environment heritability estimate of 0.16 (meta-analytical review of Little et al. 2017). The contribution of the environment to the cognitive functioning could be estimated by MZ discordant twin model. For genetically identical MZ twins, a shared environment within a family makes twins similar to each other. But a unique environment affects individual twins differently within the pair results in discordance (Asbury et al. 2016). One such example is a longitudinal study, spanning 5 years, of 55 discordant MZ pairs in literacy and numeracy (Larsen et al. 2019). It showed persistent academic discordance due to biological mechanisms, school-based factors, and personal factors. Heritability of working and spatial memory studied by a genome-wide association study (GWAS) has identified two quantitative trait loci (QTL) on chromosome 17 (Knowles et al. 2014).

The above literature review shows the heritability of human behavioral traits. They all studied one or only few aspects of the human behavior. To our knowledge, there has not been a comprehensive study of a single population across many different behavioral domains. We capitalized on the availability of a large dataset of an extended twin population with their extensive behavioral testing. We used the healthy population of young adults in HCP to determine the influence of genetics and estimate heritability across five different behavioral domains: motor, emotion, personality, sensory and cognition.

Materials and methods

Heritability calculations

Twin studies are the most powerful approach for investigating the influence of genetics and environment on human phenotypes (Jansen et al. 2015). The classical twin study compares phenotypic resemblances of MZ and DZ twins. MZ twins are derived from a single fertilized egg, and, therefore, inherit identical genetic material, while DZ twins which are derived from two different fertilized eggs. MZ twins are expected to have the greatest similarity since they are genetically identical. DZ twins share on average 50 percent of their genes (similar to ordinary full siblings) and share childhood environment, including in utero environment, to a greater degree than ordinary siblings.

Falconer's formula (Falconer 1965; Falconer and Mackey 1996) is used in twin studies to determine the genetic heritability of a trait based on the difference between intraclass correlations in MZ twins and DZ twins. Heritability is a statistic that summarizes how much of the phenotypic variation in a trait is due to variation in genetic factors. Falconer's formula h^2 defines heritability as twice the difference in the intraclass correlation of a trait between MZ and DZ twins:

$$h^2 = 2\left(\mathrm{ICC}_{\mathrm{MZ}} - \mathrm{ICC}_{\mathrm{DZ}}\right). \quad (1)$$

The rationale is that any difference between MZ twins must be environmental (non-genetic), while the difference between DZ twins is both genetic and environmental, so the difference between the two is half-genetic. In this study, Falconer's formula was used to calculate heritability in behavioral domains.

Human behavior traits emerge out of a complex and nonlinear developmental process. To understand some of these multifaceted processes, behavior measures are included in this study (see Table 1) to assess a wide range of human functions and abilities.

Participants

Participants in HCP were young healthy adults, age 22–36 years, who were free of major neurological diseases, psychiatric or medical disorders that could affect brain functioning (Marcus et al. 2013). The full set of inclusion and exclusion criteria is detailed in Van Essen et al. (2013). The final release included 1206 participants; however, since heritability is heavily dependent on known genetic relationships (twins, siblings, non-related), only participants that were genetically verified were selected for analysis. Not genetically verified participants were removed from analysis.

From the 1206 subjects, 1142 (genetically and zygosity verified) subjects were selected. To analyze and determine the heritability, behavioral data of 920 participants were grouped into the following 4 genetic groups: (a) MZ twins ($N=298$; 149 pairs), (b) DZ twins ($N=188$; 94 pairs), (c) non-twin SB ($N=358$; 147 pairs), and (d) NR ($N=76$ (not members of any other group; 38 pairs). Participants that were half siblings or siblings of twins were excluded from the analysis.

In the SB group there are, within the same family sometimes, two, three, four, or five siblings. For families with a sibling count of more than two, a pair is randomly selected for the SB group. In the NR group, individuals were randomly paired. For each measurement, for the SB and NR groups, the ICC was calculated for randomly paired individuals. After repeating this process 1001 times, the median ICC was found.

Behavioral measures

The HCP collected behavioral measures developed for the NIH Toolbox Assessment of Neurological and Behavioral function (www.nihtoolbox.org) and several additional measures to assess domains not covered by the NIH Toolbox (Barch et al. 2013). Behavioral measures assess a maximal number of wide array of functions and behaviors within a reasonable amount of time (3–4 h). Quantitative data from the following five domains were used. Non-quantifiable data have been excluded. Table 1 gives detailed information on individual behavioral traits contained in each domain.

1. *Motor (M)*: These measures quantify the participant's motor strength and skills ($N=4$).
2. *Cognition (C)*: These measures cover a wide range of cognitive functions, including episodic memory, working memory, executive function, language, and speed of cognitive processing ($N=18$).
3. *Emotion (E)*: These are self-reported measures pertaining to the emotional state and outlook of each participant, namely social relationships, psychological well-being, emotional recognition and stress ($N=24$).

Table 1 Detailed description of each of the five behavioral domains

Domain	Subdomain (measure name)
Cognition	Episodic memory (picture sequence memory) executive
	Executive function/cognitive flexibility (dimensional change card sort)
	Executive function/Inhibition (Flanker Inhibitory Control and Attention Task)
	Fluid intelligence (Penn Progressive Matrices: number correct)
	Fluid intelligence (Penn Progressive Matrices: response Time)
	Language/reading decoding (oral reading recognition)
	Language/vocabulary comprehension (picture vocabulary)
	Processing speed (pattern comparison processing speed)
	Spatial orientation (Penn Line Orientation: total number correct)
	Spatial orientation (Penn Line Orientation: total positions off for all trials)
	Spatial orientation (Penn Line Orientation: median reaction time)
	Sustained attention (Short Penn Continuous Performance Test: true positive)
	Sustained attention (Short Penn Continuous Performance Test: longest run of non-responses)
	Verbal episodic memory (Penn Word Memory Test: total number correct)
	Verbal episodic memory (Penn Word Memory Test: response time)
	Working Memory (List Sorting)
	Mean Self-regulation/Impulsivity (Delay Discounting) ((DDisc_AUC_200 + DDisc_AUC_40K)/2)
	Sustained Attention (Short Penn Continuous Performance Test: Percentage) ((SCPT_TP + SCPT_TN)/(SCPT_TP + SCPT_TN + SCPT_FP + SCPT_FN) × 100)
Emotion	Emotion recognition (Penn Emotion Recognition Test: number of correct responses)
	Emotion recognition (Penn Emotion Recognition Test: correct responses median response time
	Emotion recognition (Penn Emotion Recognition Test: correct anger identifications)
	Emotion recognition (Penn Emotion Recognition Test: correct fear identifications)
	Emotion recognition (Penn Emotion Recognition Test: correct happy identifications)
	Emotion recognition (Penn Emotion Recognition Test: correct neutral identifications)
	Emotion recognition (Penn Emotion Recognition Test: correct sad identifications)
	Negative affect (NIH Toolbox Anger-Affect Survey)
	Negative affect (NIH Toolbox Anger-Hostility Survey)
	Negative affect (NIH Toolbox Anger-Physical Aggression Survey)
	Negative affect (NIH Toolbox Fear-Affect Survey)
	Negative affect (NIH Toolbox Fear-Somatic Arousal Survey)
	Negative affect (NIH Toolbox Sadness Survey)
	Psychological well-being (NIH Toolbox General Life Satisfaction Survey)
	Psychological well-being (NIH Toolbox Meaning and Purpose Survey)
	Psychological well-being (NIH Toolbox Positive Affect Survey)
	Social relationships (NIH Toolbox Friendship Survey)
	Social relationships (NIH Toolbox Loneliness Survey)
	Social relationships (NIH Toolbox Perceived Hostility Survey)
	Social relationships (NIH Toolbox Perceived Rejection Survey)
	Social relationships (NIH Toolbox Emotional Support Survey)
	Social relationships (NIH Toolbox Instrumental Support Survey)
	Stress and self-efficacy (NIH Toolbox Perceived Stress Survey)
	Stress and self-efficacy (NIH Toolbox Self-Efficacy Survey)
Motor	Endurance (2-min walk test)
	Locomotion (4-m walk test)
	Dexterity (9-hole Pegboard)
	Strength (Grip Strength Dynamometry)

Table 1 (continued)

Domain	Subdomain (measure name)
Personality	Five Factor Model NEO-FFI (agreeableness)
	Five Factor Model NEO-FFI (openness)
	Five Factor Model NEO-FFI (conscientiousness)
	Five Factor Model NEO-FFI (neuroticism)
	Five Factor Model NEO-FFI (extroversion)
Sensory	Audition (Words in Noise)
	Olfaction (Odor Identification Test)
	Pain (Pain Intensity and Interference Surveys) (self-report)
	Taste (Regional Taste Intensity Test)
	Contrast Sensitivity (Mars Contrast Sensitivity)

4. *Personality (P)*: These measures come from the 60-item version of the Costa and McCrae Neuroticism/Extroversion/Openness/Agreeableness/Conscientiousness Five Factor Inventory (NEO-FFI) ($N=5$).
5. *Sensory (S)*: These measures cover the following sensory modalities: visual activity, contrast, and color, audition, olfaction, pain and taste ($N=5$).

Statistical analyses of ICC and heritability

ICC

ICC and its z-transform zICC were computed for each measure. Negative ICC values are outside the theoretical range for an ICC, although such values are mathematically possible. When interpreting negative ICC values in the context of estimating inter-rater reliability, it is advised, "there is no other possible interpretation but poor agreement" across raters (Giraudeau 1996). Therefore, in these cases, the value was excluded.

Fisher's (Fisher 1958) r to z transformation was conducted to fit ICC variable to a normal probability distribution. Then mean z-transformed ICC (zICC) for each genetic group and domain were calculated.

Multidimensional scaling (MDS)

MDS is a powerful tool to identify relations among items in a multidimensional space. It is a dimensionality reduction method used to reduce the number of dimensions in a multidimensional data set, typically to two or three dimensions. The input to MDS is a proximity (square) matrix, which typically consists of pairwise dissimilarities between items. MDS places the items in a low-dimensional space such that the distances between items in this space are as close as possible to their corresponding distances in the original space. The derived plot captures arrangements of items that share common attributes in the reduced space and thus may reveal associations hitherto unsuspected. In this analysis, the nonmetric MDS implemented in the IBM-SPSS (version 26) package was used.

Hierarchical tree clustering (HTC)

HTC is a multivariate method that places items in hierarchically organized clusters, forming a tree (dendrogram). HTC assumes the presence of a root, which, in this proposal, is the heritability, i.e. that items to be clustered are all heritabilities. HTC organizes objects into a dendrogram and clusters are defined by cutting branches off the dendrogram (Langfelder et al. 2008). The hierarchical clustering process looks for pairs of samples that are the most similar. The input is a dissimilarity matrix; therefore, the pair that has the lowest dissimilarity is the most similar. The point at which the pairs are joined is called a node. This step keeps repeating and the dissimilarity is recalculated between each merged pair and other samples. The analysis will use between-groups linkage and squared Euclidean distance to compute a dendrogram using the IBM-SPSS (version 26) package.

Results

Out of genetically confirmed healthy young (age range 22–36) participants, twin data consisted of individuals comprising MZ twins, DZ twins, non-twin siblings and unrelated individuals. The descriptive statistics of age and gender of four groups of participants are given in Table 2. Test scores were analyzed from 56 traits in 5 domains (motor, sensory, cognition, emotion, and personality).

Table 2 Demographics of the participants

	MZ	DZ	SB	NR
Total *N*	298	188	358	76
Male *N*	124	68	182	41
Female *N*	174	120	176	35
Age mean (SD)	29.3 (3.3)	29.3 (3.5)	27.9 (3.7)	28.5 (3.9)
Male age mean (SD)	27.8 (3.3)	27.0 (3.2)	27.8 (3.6)	27.6 (3.9)
Female age mean (SD)	30.3 (2.9)	30.6 (2.8)	28.1 (3.9)	29.5 (3.9)

MZ monozygotic twins, *DZ* dizygotic twins, *SB* non-twin siblings, *NR* non-related participants, *N* number, *SD* standard deviation

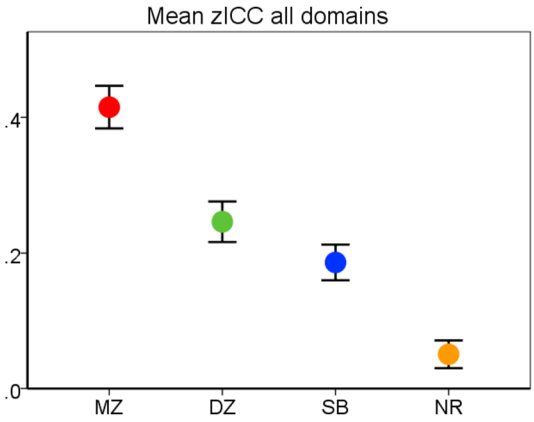

Fig. 1 Mean zICC ± SEM per genetic group. *MZ* monozygotic twins (*N* = 298, 149 pairs), *DZ* dizygotic twins (*N* = 188, 94 pairs), *SB* non-twin siblings (*N* = 358, 147 pairs), and *NR* non-related participants (*N* = 76, 38 pairs)

Details are shown in Table 1. Specifically, four analyses were carried out.

Intraclass correlations

First, the mean zICCs was calculated for each genetic group and trait from the z-transformed ICCs. Figure 1 presents mean zICCs for genetic groups. The highest zICC are for MZ twins, smaller zICCs for DZ and SB, and near zero for NR. One-way ANOVA was used to estimate the difference between four groups of participants. For each brain group, zICC as an independent variable and groups of participants as a factor, ANOVA showed high statistical significance ($P < 10^{-16}$). MZ twins also had consistently and significantly higher zICC than that of DZ and also that of SB groups (P value < 0.05) suggesting again strong genetic influence. The mean zICCs were close to zero for the NR group, as would be expected for unrelated individuals.

Participants were also split by gender and the same systematic variation was observed (Figs. 2 and 3). A specific comparison of the zICC between DZ and SB groups, since those pairs share the same amount (50%) of genetic material, was performed. The zICC of these groups did not differ significantly ($P = 0.123$, ANOVA).

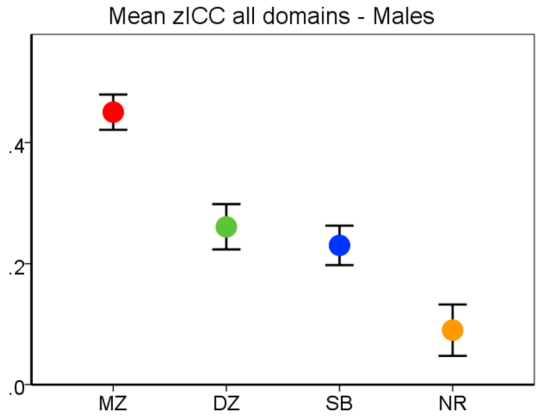

Fig. 2 Mean zICC ± SEM per genetic group males. *MZ* male monozygotic twins (*N* = 124, 62 pairs), *DZ* male dizygotic twins (*N* = 68, 34 pairs), *SB* male non-twin siblings (*N* = 113, 51 pairs), and *NR* male non-related participants (*N* = 41, 20 pairs)

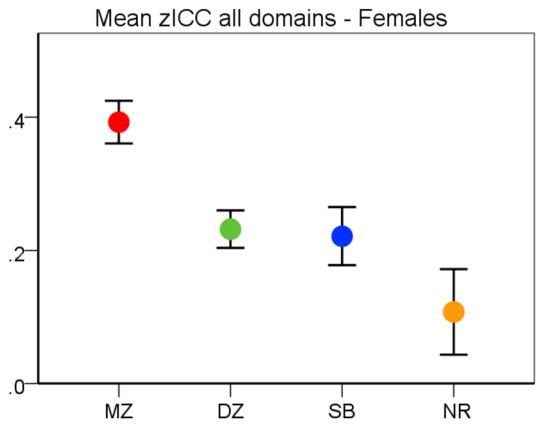

Fig. 3 Mean zICC ± SEM per genetic group females. *MZ* female monozygotic twins (*N* = 174, 87 pairs), *DZ* female dizygotic twins (*N* = 120, 60 pairs), *SB* female non-twin siblings (*N* = 107, 50 pairs), and *NR* female non-related participants (*N* = 35, 17 pairs)

Heritability

Heritability (h^2) was computed for each domain to compare heritabilities across domains; negative heritabilities were removed. The mean heritability values for the five domains were: cognition $h^2 = 0.405$, emotion $h^2 = 0.316$, motor $h^2 = 0.138$, personality $h^2 = 0.444$, and sensory $h^2 = 0.193$. Next we calculated heritability separately for male and female groups. For males, the heritability values were: cognition $h^2 = 0.483$, emotion $h^2 = 0.360$, motor $h^2 = 0.294$, personality $h^2 = 0.364$ and sensory $h^2 = 0.669$.

For females, the heritability values were: cognition $h^2 = 0.364$, emotion $h^2 = 0.301$, motor $h^2 = 0.132$, personality $h^2 = 0.561$ and sensory $h^2 = 0.237$.

The probability–probability plot of heritability values, under the assumption of a normal distribution, deviated from normality, as indicated by the deviation of the plotted values from the midline (Fig. 4 top), whereas the log-transformed heritability values were very close to a normal distribution (Fig. 4 bottom). Therefore, we used log-transformed heritability values in ANOVA. Overall, significant difference was found among behavioral domains ($F_{[4,44]} = 3.499$, $P = 0.014$, ANOVA, Fig. 5). In addition, pairwise comparisons showed that the motor domain was significantly different from: (1) cognitive ($P = 0.002$), (2) personality ($P = 0.003$), and (3) emotion ($P = 0.013$) domains.

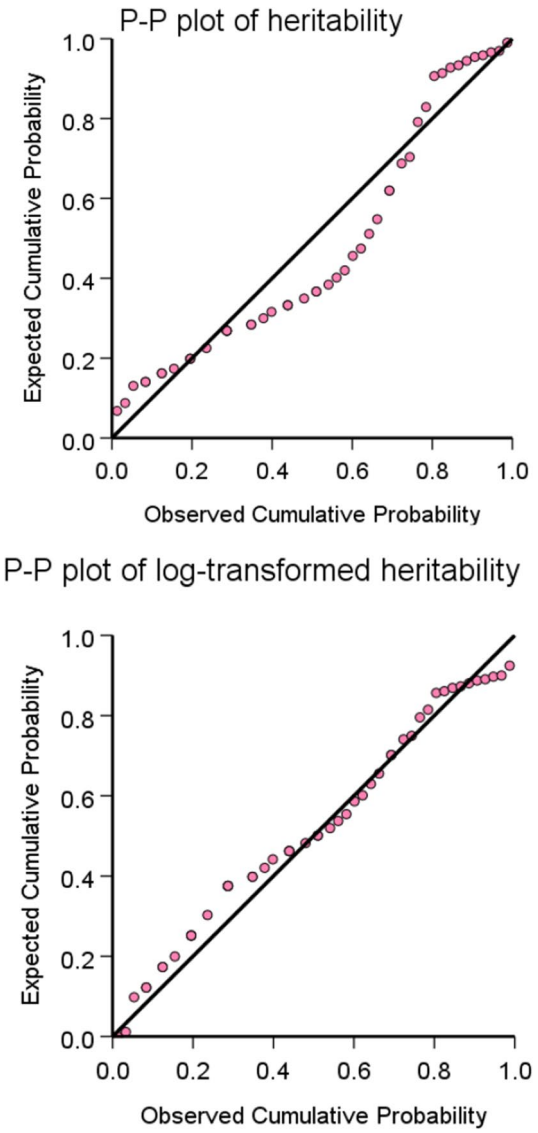

Fig. 4 The probability–probability (P–P) plot under the assumption of a normal distribution. Top: P–P plot of heritability values deviated from normality indicated by the deviation of the plotted values from the midline. Bottom: P–P plot of log-transformed heritability values very close to a normality, indicated by the plotted values close to the midline

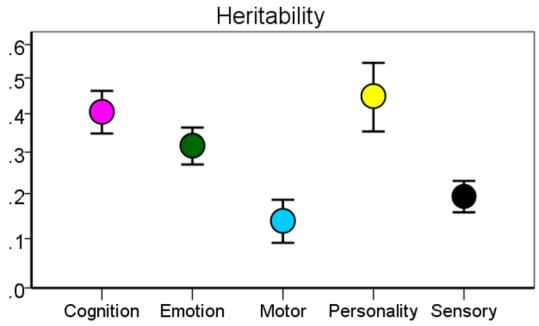

Fig. 5 Mean $h^2 \pm$ SEM per behavioral domain: cognition ($N = 16$), emotion ($N = 20$), motor ($N = 4$), personality ($N = 5$), and sensory ($N = 4$)

Multidimensional scaling

Third, the MDS analysis of the behavioral domain heritabilities (Fig. 6) revealed a separation of the five domains in four quadrants comprising motor and sensory domains (upper and lower right quadrant), emotion and cognition (lower left), and personality (upper left). The fit of the nonmetric (ordinal) model was excellent (normalized raw stress = 0.00004, dispersion accounted for = 0.99).

Hierarchical tree clustering

Finally, the grouping and gradient above was confirmed in the HTC dendrogram (Fig. 7), which comprises two branches, one containing motor and sensory in one branch and in two separate sub-branches, emotion in one branch and

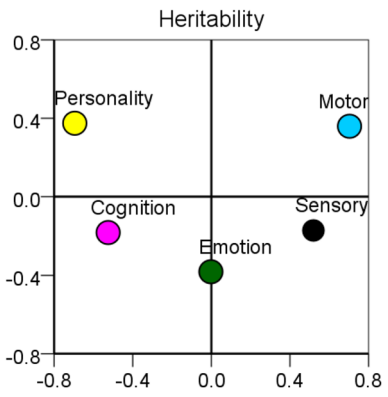

Fig. 6 Multidimensional scaling of median h^2 of the five behavioral domains: cognition ($N = 16$), emotion ($N = 20$), motor ($N = 4$), personality ($N = 5$), and sensory ($N = 4$)

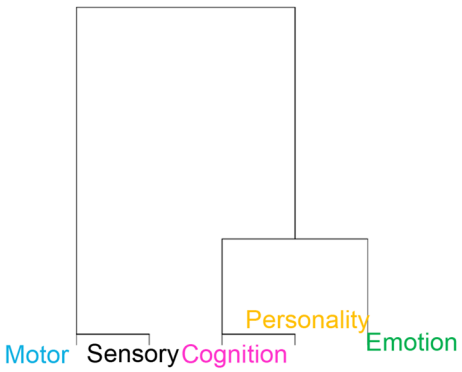

Fig. 7 Hierarchical tree clustering dendrogram of the dissimilarity matrix for the five behavioral domains: cognition ($N=16$), emotion ($N=20$), motor ($N=4$), personality ($N=5$), and sensory ($N=4$)

the other containing cognition and personality in a single branch.

Discussion

Here we presented the results of a comprehensive study of a single population across many different behavior domains. We used known genetic and family relationships, and their behavioral test results in a young, healthy population to determine the influence of genetics and heritability across five different behavioral domains: motor, emotion, personality, sensory, and cognition. The data set we used is the freely available HCP battery of measures, obtained in a reasonable time (3–4 h), for varieties of human behavior and functions. Both NIH toolbox behavioral, Non-NIH toolbox, and self-repot measures are well validated and reliable (Barch et al. 2013).

HCP data set includes MZ and DZ twins, non-twin siblings and non-related participants. Twins are invaluable for the estimation of heritability as they can separate the contribution of genes versus environment. In classical twin studies, the basic assumptions are that MZ twins share on average 100% of their alleles, while DZ twins share on average 50% of their alleles, and both MZ and DZ twins share a common environment. One method for calculating heritability is to use Falconer's formula. When one uses this formula, there is an assumption that unique environment contributes equally to the phenotypic variance for both MZ and DZ twins. This means that the difference between MZ phenotypic correlation and DZ phenotypic correlation is due to genetic factors (Mayhew and Meyre 2017; Polderman et al. 2015). Maximum likelihood-based modeling estimates various components for the total variance (Martin and Eaves 1977; Winkler et al. 2015), but in essence relies on the same set of logic and assumptions.

An age effect has been shown for virtually all behavioral domain (King et al. 2019; Briley and Tucker-Drob 2013; Haworth et al. 2010). It is shown that the cognitive, motor and other abilities are still developing, progressing and enriching during childhood and adolescence with unique patterns (Feinstein and Bynner 2004; Luna et al. 2004; Zhang et al. 2018). For example, cognitive ability increases linearly and significantly from 41% in childhood to 55% in adolescence and to 66% in young adulthood (Haworth et al. 2010). In contrast, late adulthood is a period where abilities progressively decline. For example, Zhang et al. (2018) showed age-related decline of human memory. Additionally, the review of Plomin and Deary (2015) showed that the heritability of intelligence, one of the most heritable behavioral traits, changes with age. It increases from 20% in infancy to 80% in later adulthood. The above evidences are supporting the argument that age has a strong influence on behavioral performance that is why the age related changes of heritability has to be accounted for. The participants of the HCP were young healthy adults with a relatively narrow age range. Moreover, they were in the peak of their behavioral skills and abilities at age after developmental stage but before age related changes and decline. This relatively narrow age range population led to more consistent findings. The results of healthy adults group could be used as a base for comparisons with people with neurological and psychiatric abnormalities, and with other age groups: development or elderly age groups.

The grouping of participants into genetic groups of MZ twins, DZ twins, non-twin siblings, and non-related individuals resulted in the zICC differing significantly and varying systematically among the groups. The zICC for MZ twins is the highest, followed by zICC for DZ twins, smaller value for zICC of SB, and zero for NR for all behavioral measurements. This result is expected and is consistent with the literature since MZ twins share all genetic effects, while DZ twins share on average 50% of their genetic effects. Siblings also share, on average, 50% of their genetics; however, it is expected that they would have lower zICC and heritability values because their environmental variation is higher compared to twins. The non-related participants are expected to be last in terms of similarity since they are not expected to have any genetic effects.

Our heritability results are in agreement with the literature: most human behavioral traits have some degree of heritability across different domains (Johnson 2011; Turkheimer 2000). Overall, significant difference was found among log-transformed heritabilities of behavioral domains (Fig. 5, $P=0.014$). Whereas seven out of ten pairwise domain comparisons showed no statistical significance. A hypothesis for this is that heritability relates to overlapping brain biology/function and shares converging brain networks.

Overall, heritability differed significantly. Three pairwise comparisons: motor–cognitive, motor–personality, and motor–emotion were also significantly different. The motor domain heritability was the lowest of all, and was also significantly lower than the heritability of cognitive, personality, and emotion domains. A possible explanation is that these behavioral domains have an entirely different nature. The motor domain measures physical ability, while cognition, personality, and emotion are a more brain-based feature. Specifically, physical skills like muscle strength and skills to perform tasks are included in the motor domain, while memory, executive functions, and language are part of the cognitive domain. Human behavior across situations is described by the personality domain while an affective state of consciousness when strong feelings are experienced is part of the emotion domain.

Our value for the heritability of combined emotion traits are close to the heritability of ability to recognize specific emotion reported by Rappaport et al. (2018). In this paper, personality heritability estimates are similar to that in the literature (Power and Pluess 2015) including the findings of the massive meta-analysis of Vukasovic and Bratko (2015). For the cognitive traits, we found very similar values to the results obtained by other authors. Han and Adolphs (2020) also used the Falconer's formula on the similar subset of HCP behavioral data specifically for the psychological measures and found results similar to ours. For the contribution of genetic to variation in spatial ability, King et al. (2019) found higher values than ours.

Our results cannot be directly compared with that reported in the literature because in other studies, usually one or only few behavioral traits were studied while we look at the compound of at least four or many behavioral measures per domain.

In summary, our heritability results are in agreement with the literature: most human behavioral traits have some degree of heritability across different domains (Johnson 2011; Turkheimer 2000). For those behavioral domains with no pairwise difference, the hypothesis that heritability relates to overlapping brain biology/function is a possible explanation. We found that the motor domain was significantly different from the cognitive, personality, and emotion domains. A possible explanation for this result and for the overall difference is that motor, emotion, personality, sensory, and cognition domains describe completely different human abilities and behaviors.

When the participants were split by gender, the overall pattern was followed by all domains for males and females. One hypothesis could be that that this finding reflects the shared neural substrates among genders.

MDS and HTC were used to decipher grouping of the heritabilities based on domain. Splitting the MDS graph by the dimension in *x*-axis, would position motor–sensory on the right side of the graph and cognition–personality on the left side of the graph with emotion in the middle. This can be interpreted that the relevant gradient extends from simple, sensory–motor domains to complex, cognitive–affective domains. This grouping of the MDS is further confirmed in the HTC results. For example, a genetic interpretation could be that the motor and sensory areas of the brain were influenced by the similar genetic factor, whereas the cognition, personality, and emotion areas were influenced by a different genetic factor. Additionally, emotions can be separated from cognition, personality probably influenced differently. Hence, there is an overlap in genes regulating processes of cognition, personality, and emotion, while other genes play a role in the sensory–motor functioning area (Polderman et al. 2015).

These analyses yielded substantial new information on the effects of genetics on behavior, and partially elucidated underlying associations among the various diverse behavioral measures. To our knowledge, this is the first such comprehensive study carried out.

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