Social behavior in young twins : are fearfulness, prosocial and aggressive behavior related to frontal asymmetry?

Wijk, I.C. van

CHAPTER 2

Behavioral genetics of temperament and frontal asymmetry in early childhood

Ilse C. van Wijk, Rens Huffmeijer, Jizzo R. Bosdriesz, Marian J. Bakermans-Kranenburg, Laura Kolijn, Marinus H. van IJzendoorn, Claudia I. Vrijhof, & Bianca G. van den Bulk

Published in Journal of Experimental Child Psychology (2019), 179, 348–361

Abstract

Temperament has been suggested to be influenced by genetic and environmental factors. The current study examined genetic shared environmental and unique environmental factors accounting for variation in Fear, Effortful Control (EC), and Frontal Asymmetry (FA) in 4- to 6-year-old children using bivariate behavioral genetic modeling. We included a total of 214same-sex twin pairs: 127monozygotic (MZ) and 87 dizygotic (DZ) pairs. FA was measured during a rest electroencephalogram (EEG) recording, and Fear and EC were measured using parent report. Results show that differences between twins were best explained by genetic factors (about a quarter of the variance) and unique environmental factors (about three quarters of the variance). However, the cross-trait, within-twin correlations were not significant, implying no overlapping genetic or environmental factors on Fear and EC or on Fear and FA. Future research should try to elucidate the large role of unique environmental factors in explaining variance in these temperament-related traits.

Keywords: Temperament; frontal EEG asymmetry; behavioral genetics; early childhood

Introduction

Each child has his or her own unique temperament, which affects how the child reacts to the world. Some children will approach new situations with joy, whereas others will be more reluctant. This has a great impact on their development, and that is why temperament is one of the most widely studied features in child development (Buss & Plomin, 2014; Zentner & Shiner, 2015). Temperament has been suggested to be influenced by genetic and environmental factors form birth onward (Zentner & Shiner, 2015) and is suggested to be associated with electroencephalogram (EEG) Frontal Asymmetry (FA), the difference in activation between the left and right frontal brain areas (Rothbart, 2011). FA is related to approach and withdrawal tendencies (Harmon-Jones, Gable, & Peterson, 2010), and temperament is linked to (the modulation of) approach and withdrawal behavior (Diaz & Bell, 2012; Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; Rothbart, 2011; Smith, Diaz, Day, & Bell, 2016). Studies have shown that in particular Fear may be related to FA. More fearfulness has been related to greater right frontal activity (Fox et al., 2001; Howarth, Fettig, Curby, & Bell, 2016). In addition, studies have shown a relation between Fear and Effortful Control (EC; Cole, Zapp, Fettig, & Pérez-Edgar, 2016; Hill-Soderlund & Braungart-Rieker, 2008; Kiff, Lengua, & Bush, 2011). In the current study, we examined the associations among Fear, EC, and resting FA and explored whether temperamental features and FA are influenced by distinct or overlapping genetic and environmental factors in early childhood. Therefore, we investigated the genetic and environmental factors accounting for variation in Fear and EC, as well as in Fear and resting FA, in a sample of 4- to 6-year-old same-sex twins using bivariate behavioral genetic modeling.

The temperamental factor Fear indicates how nervous or worried a child is in relation to anticipated pain, distress, or threatening situations. Children's fearfulness can result in withdrawal behavior, for example, in a social context (Coplan, Prakash, O'Neil, & Armer, 2004; Fox et al., 2005; Henderson, Marshall, Fox, & Rubin, 2004). Infants already show fearful behavior very early in life, and experiencing fear is thought to be normal in childhood (Field & Davey, 2001; Gullone, 2000). Although the stimuli and situations that elicit fear in children change

over time and both the intensity and prevalence of fear seem to decrease with age, stable individual differences in fearfulness are observed later in infancy (Gullone, 2000; Rothbart & Bates, 2006). Another important dimension of temperament is effortful control, defined as "the efficiency of executive attention, including the ability to inhibit a dominant response and/or to activate a subdominant response, to plan, and to detect errors" (Rothbart & Bates, 2006, p. 129). EC can be assessed by using parent report or behavioral measures of attentional focusing and inhibitory control (Rothbart, 2011). The development of EC starts at the end of the first year of life (Kiff, Lengua, & Zalewski, 2011), and although abilities for control continue to develop, individual differences stabilize at around 3 years of age (Kochanska, Murray, & Harlan, 2000). In support of this finding, individual differences in EC were found to be relatively stable in childhood (i.e., between 3 and 14 years of age; Tiberio et al., 2016).

Fear and EC both are part of child temperament and are suggested to be related. In addition, EC seems to play an important role in the development of emotion regulation (Rothbart & Bates, 2006) given that EC is involved in the expression of emotion. For example, in a scary or threatening situation, individuals with low EC may show high levels of fearful withdrawal behavior, whereas high EC may cause individuals to approach the situation and reduce anxiety. Studies with children have shown this association between Fear and EC; fearful infants (8–16 months old) had lower EC in early childhood (4.5–5.5 years) (Hill-Soderlund & Braungart-Rieker, 2008), social withdrawal was negatively correlated with EC in 4- to 7-year-olds (Cole et al., 2016), and Fear was negatively correlated with EC in 8- to 12-year-olds (Kiff et al., 2011). Because Fear and EC both are related to child temperament and studies have shown associations between the two traits, we tested whether the same genetic and/or environmental factors are involved in Fear and EC. We were specifically interested in estimating genetic and environmental influences in early childhood given that both Fear and EC individual differences are found to be stable from around 3 years of age (Gullone, 2000; Kochanska et al., 2000; Rothbart & Bates, 2006; Tiberio et al., 2016).

Many previous studies have used behavioral data (e.g., questionnaires, observations) to examine Fear and EC (Cole et al., 2016; Coplan et al., 2004; Fox et al., 2005; Gullone, 2000; Henderson et al., 2004; Rothbart, Ahadi, Hershey, & Fisher, 2001). However, with neurophysiological measures like FA, it is also possible to measure specific underlying behavioral tendencies (Harmon-Jones et al., 2010; Rothbart, 2011). FA is usually measured as the difference in EEG alpha power over the left and right frontal hemisphere. Research has shown that motivational tendencies are robustly related to FA; approach behavior is related to greater left than right frontal cortical activity, whereas withdrawal behavior is linked to greater right than left frontal cortical activity (Harmon-Jones & Gable, 2018; Harmon-Jones et al., 2010). Several studies have suggested relations among Fear, withdrawal, and relatively greater right FA during rest in adults (Mathersul, Williams, Hopkinson, & Kemp, 2008; Neal & Gable, 2017; Tomarken, Davidson, & Henriques, 1990), infants, and children (Fox et al., 2001; Schmidt, 2008). However, developmental samples have shown inconsistent results for the relation between Fear and FA (Diaz & Bell, 2012; Howarth et al., 2016; LoBue, Coan, Thrasher, & DeLoache, 2011). Still, FA might represent the neurophysiological mechanism underlying the withdrawn and avoidant behavior patterns resulting from Fear. A meta-analytic review indeed reported that depression and anxiety, factors that are linked to Fear, are also related to relatively greater right frontal brain activity (Thibodeau, Jorgensen, & Kim, 2006). We examined whether the same genetic and/or environmental factors are involved in Fear and FA. The direct relation between EC and FA is less well studied (cf. Kim & Bell, 2006; Smith et al., 2016). Although one study obtained a direct relation between EC and FA in children (Kim & Bell, 2006), EC might influence the relation between Fear and FA. For instance, in children with high EC, the relation between Fear and FA might be weaker because high control may enable children to overcome their fears and confront, rather than withdraw from, a scary situation. In the current study, we examined the possible modulating role of EC by computing partial correlations between Fear and FA while controlling for EC. Substantial differences between the bivariate correlations (between Fear and FA) and the partial correlations would indicate an influence of EC on the association between Fear and FA.

Behavioral genetic studies have suggested that a substantial amount of variance in Fear and EC can be explained by genetic factors (Goldsmith, Buss, & Lemery, 1997; Van Houtem et al., 2013). For example, researchers have estimated that genetic factors accounted for 74% and unique environmental factors for 26% of variance in individual differences in parent-reported Fear in 8-year-old children (Clifford, Lemery-Chalfant, & Goldsmith, 2015). Regarding EC, one study indicated that dominant genetic factors accounted for 68% and unique environmental factors for 32% of variance in parent-reported EC in 8-year-olds (Lemery-Chalfant, Doelger, & Goldsmith, 2008).

Only a few studies have investigated the behavioral genetics of FA. In female adult participants, genetic factors were estimated to account for 27% of the variance and unique environmental factors for 73% of the variance in FA (Anokhin, Heath, & Myers, 2006). A study in young adults found that genetic factors accounted for 32% (in men) and 37% (in women) of individual differences in FA (Smit, Posthuma, Boomsma, & De Geus, 2007). Moreover, Smit et al. (2007) examined the relation between FA and risk for anxiety and depression (also related to fearfulness as described above) in a bivariate genetic analysis. They found that FA and the risk for anxiety/depression correlated significantly only in a subsample of young women and concluded that the correlation was explained by overlap in genetic factors. The influence of genetic shared and unique environmental factors on characteristics such as Fear, EC, and FA, however, changes over the lifespan (Briley & Tucker-Drob, 2014; Kandler & Papendick, 2017; Scaini, Belotti, & Ogliari, 2014), and research in young children is lacking. Conducting behavioral genetic research with a focus on developmental populations will, therefore, add important information to the current literature.

We conducted a twin study including 4- to 6-year-old same-sex twins to examine the behavioral genetics of Fear, EC, and FA using bivariate behavioral genetic modeling. Because previous research has suggested associations between Fear and EC and between Fear and FA (Cole et al., 2016; Fox et al., 2001; Hill-Soderlund & Braungart-Rieker, 2008; Howarth et al., 2016; Kiff et al., 2011; Rothbart, 2011; Schmidt, 2008), we were interested in the extent to which the

same and/or different genetic and environmental factors account for variation in these temperamental characteristics.

Method

Participants

Participants took part in a larger longitudinal intervention study of the Leiden Consortium on Individual Development (L-CID; Euser et al., 2016). We recruited families with same-sex twins born between 2010 and 2013 via municipal authorities in the western part of The Netherlands. Children with disabilities or neurological impairments that prevented them from completing the tasks were excluded (i.e., congenital disability, psychological disorder, chronic illness, hereditary disease, or visual or hearing impairment). For the current study, we used data from the second wave of the data collection in which 215 twin pairs participated. We asked both parents from each family to take part in the study. The primary parent (i.e., the parent who spends the most time with the children) was invited for each visit and asked to complete a set of questionnaires; in most cases (94%), the primary parent was the biological mother of the twins. The other parent was asked to complete questionnaires as well.

One twin pair was excluded from the analyses because of missing data on all variables used in the current study. Another 12 participants had missing data for Fear and EC because both parents did not complete the Child Behavior Questionnaire (CBQ; Rothbart et al., 2001). There was also missing data on FA (in total 102 incomplete or missing twin pairs) because of insufficient artifact-free EEG data (n = 50), technical problems during EEG acquisition (n = 29), or refusal to wear the EEG net (n = 61). All participants (also with partially missing data) could be included in the behavioral genetic analysis because it employs full information maximum likelihood (FIML) modeling, which can deal with missing data. FIML estimates a likelihood function for each individual in the dataset based on all variables with valid data (Enders, 2001). The final sample, therefore, consisted of 214 twin pairs, 127 of which were monozygotic (MZ) and 87 of which were dizygotic (DZ). Zygosity was determined by analyses of DNA samples

collected by buccal swabs. When the DNA samples were missing, zygosity was based on the zygosity questionnaire (Rietveld et al., 2000), which was filled out by the primary parent. The mean age of the MZ twins was 4.82 years (SD = 0.61, confidence interval (CI) [3.86–6.54]) and of the DZ twins was 4.70 years (SD = 0.53, CI [3.93–6.14]). See Table 1 for participant characteristics.

Both parents provided written informed consent at the start of the study, and study procedures were approved by the local ethics committee and the Central Committee on Research Involving Human Subjects in The Netherlands (No. NL49069.000.14, "Samen Uniek"). Participating families received financial reimbursement after each visit, and the children received a small gift.

Table 1. Participant characteristics

	MZ twins	DZ twins
N (total twin pairs)	127	87
Girls (%)	51%	53%
Mean age in years (SD)	4.82 (.61)	4.70 (.53)
Age range	3.86 – 6.54	3.93 – 6.14

Procedure

Families were invited to the lab at Leiden University. One week before the lab visit, the parents received an e-mail asking them to complete several online questionnaires, including the CBQ (Rothbart et al., 2001). During the lab visit, each co-twin was randomly assigned to one of two order conditions (starting with a block of behavioral tasks or EEG measures) and to a research assistant who supervised the tasks and motivated the child throughout the test session. One block of tasks consisted of EEG measures, including a baseline and task EEG measurements. The other block included several behavioral tasks and parent–child interaction tasks (results reported elsewhere). After completing the first block of tasks, the participants switched rooms

and completed the other block of tasks. The total duration of the lab visit was approximately 3 h. At the start of the block including the EEG measurement, the procedure was explained to the parent and child by the experimenter. Next, the child was fitted with the electrode net. The first measurement was a 3-min resting baseline EEG measurement (see below). Next, a task lasting approximately 15 min was conducted (results presented elsewhere; van Wijk et al., 2017).

Measures and data processing

Child behavior questionnaire. To measure child temperament, parents completed the subscales Fear (12 items), Attentional Focusing (short form, 6 items), and Inhibitory Control (short form, 6 items) of the CBQ for each cotwin separately. Together, the subscales Attentional Focusing and Inhibitory Control form the dimension Effortful Control (EC). Items were rated on a 7-point Likert scale ranging from extremely untrue for your child (1) to extremely true for your child (7). When the behavior described in the item was not previously observed in the child, it was rated as not applicable (8). These items were coded as missing values and were not included in subscale scores. Previous studies have shown acceptable internal consistency of the subscales: Fear a = .70, Attentional Focusing a = .75, and Inhibitory Control a = .72 (Putnam & Rothbart, 2006; Rothbart et al., 2001).

To limit the number of questions for the parent, we used planned random missing items in the CBQ (Graham, Taylor, Olchowski, & Cumsille, 2006; Little & Rhemtulla, 2013). For both the subscale Fear and the dimension EC, 3 items were always included, and of the remaining 9 items, 6 items were randomly selected to be included for each co-twin. Missing value analyses confirmed that data were missing completely at random (MCAR); p values for Little's MCAR test (Little & Rubin, 1989) ranged between .18 and .77. We used multiple imputation (Rubin, 1987; Schafer & Olsen, 1998) in SPSS 23 (IBM, Armonk, NY, USA) to handle missing items. A total of 100 imputed datasets were generated for each subscale, for each parent, and for each child separately (the oldest and youngest co-twins within families were randomly assigned to Twin Group A or Twin Group B). The average Cronbach's alpha for the imputed data of the

primary parent was M = .73 for Fear and M = .82 for EC. For the other parent, the average Cronbach's alpha of the imputed data was M = .64 for Fear and M = .82 for EC. Total scores were then computed for Fear and EC for each dataset, and the datasets were pooled and merged. The pooled total scores for Fear and EC were used in subsequent analyses.

The correlations for Fear and EC between the pooled scores from the primary parent and the other parent were substantial and significant (Fear: Child 1 $r = .47$ and Child 2 $r = .52$; EC: Child 1 $r = .51$ and Child 2 $r = .52$, all $ps < .01$). Because a paired-samples t test showed one significant difference between the primary parent and the other parent on EC Child 2, $t(157) = 3.07$, $p < .01$, we used the standardized values to compute a mean score based on both parents' ratings on Fear and EC, which we used in further analyses. When one of the parents did not fill out the CBQ ($n = 17$ for the primary parent and $n = 45$ for the other parent), the score of the parent who did fill out the CBQ was used in further analyses (which is taken into account by computing the mean score). Both Fear and EC were normally distributed (z skewness and z kurtosis values did not exceed ±3), and there were no outliers (all $|z| < 3.29$).

Frontal EEG asymmetry. EEG was recorded during a 3-min resting baseline. The child was instructed to alternatingly open or close his or her eyes for 30 s each (3x30 s eyes open and 3x30 s eyes closed). The computer played an audio message telling the child to close his or her eyes and displayed a drawing of closed eyes when the child needed to close the eyes. After 30 s, an audio message was played saying that the child could open his or her eyes again. During the eyes open trials, the child saw a color-changing dot on the screen to focus attention and avoid excessive eye movements.

A 64-channel HydroCel Geodesic Sensor Net and NetStation software (Electrical Geodesics, Eugene, OR, USA) with a NetAmps300 amplifier were used to record the EEG. To ensure a good signal, each electrode was adjusted to keep impedances below 100 kO. To avoid fatigue, irritability, and loss of attention in young children, we minimized preparation time by adjusting and collecting data from only a subset of the electrodes (number in brackets): F3

[12], F4 [60], F7 [18], F8 [8], C3 [20], C4 [50], T7 [24], T8 [52], P3 [28], P4 [42], P7 [30], P8 [44], left [29] and right [47] mastoids, and two electrodes [62, 63] placed directly below the eyes. During recording, the reference was Cz and data were low-pass filtered at the Nyquist frequency (i.e., 100 Hz) for the sampling rate of 250 Hz. After applying a 0.3-Hz high-pass filter (99.9% pass-band gain, 0.1% stop-band gain, 1.5 Hz roll-off), data were exported for further processing using Brain Vision Analyzer (BVA) 2.0 software (Brain Products GmBH, Gilching, Germany). The EEG was low-pass filtered at 30 Hz (-3 dB, 48 dB/octave) and Cz was used as reference. The six 30-s trials were segmented into 2-s segments with 1-s overlap. Segments containing artifacts (i.e., segments in which the difference between the largest and smallest values was larger than 200 lV or in which the difference between the largest and smallest values within any 100-ms interval was smaller than 0.5 lV in any channel) were removed, and bad channels were deleted from an individual dataset if the channel contained artifacts in more than 50% of segments. A fast Fourier transformation (0.5 Hz resolution, 100% Hamming window) was used to compute power values (lV2). Power values were averaged per condition over the artifact-free segments. The minimum requirement for a child's data to be included in further analyses was 28 segments per condition (equal to 56 s over the two conditions). On average, 63 segments per condition were included (eyes closed: M = 61, CI [29–87]; eyes open: M = 65, CI [29–87]).

Power values were then averaged across the frequency range of 6–10 Hz (alpha power in young children; Marshall, Bar-Haim, & Fox, 2002) to obtain alpha power for each condition. With a natural log transformation, the data distributions were normalized. Based on other studies of FA (for a review, see Coan & Allen, 2004) and studies that specifically investigated the contribution of genetic and environmental factors to FA (Anokhin et al., 2006; Smit et al., 2007), we used electrodes F4 and F3 to compute FA. Other electrode sites were not analyzed. Alpha activity over left frontal areas (electrode F3) was subtracted from alpha activity over right frontal areas (electrode F4) to compute FA. The data showed four outliers ($|z| > 3.29$) that were winsorized (Tabachnick & Fidell, 2006). To check the reliability of our FA measure, we computed split half reliability; FA was computed separately for odd and even segments (following the same procedures as described above), and intraclass correlations between

measures for odd and even segments were computed. Results showed high intraclass correlation coefficients (condition eyes open: Child 1 $r = .86$, $p < .01$ and Child 2 $r = .90$, $p < .01$; condition eyes closed: Child 1 $r = .88$, $p < .01$ and Child 2 $r = .90$, $p < .01$), indicating that the measurement was reliable and did not show much variance. Furthermore, the correlation between FA in the two conditions (eyes open and eyes closed) was high ($r = .87$, $p < .001$). Therefore, we decided to average across the two conditions to obtain one value of FA per child, which we used in all subsequent analyses.

There were 42 children with sufficient artifact-free EEG data for one condition only (eyes open [n = 33] or eyes closed [n = 9]). To enhance the number of twin pairs included in our study and because of the high correlation between the eyes open and eyes closed conditions ($r = .88$, $p < .01$), we estimated the value of the missing condition based on the value of the other condition using the regression equation obtained in the subsample of children with sufficient data for both conditions (n = 246). Using this method, data of 22 twin-pairs could be imputed and included in the bivariate behavioral genetic modeling analyses.

Data analyses

Individual differences in phenotype can be accounted for by genetic (A), shared environmental (C), and unique environmental (E; also includes measurement error) factors. These factors can be quantified using a twin ACE model because MZ and DZ twins differ in their genetic relatedness; MZ twins share virtually 100% of their structural genome and, thus, have a correlation of 1 in their genetic factors, whereas DZ twins share on average 50% of their genome and, thus, have a correlation of .50. Shared environmental factors are events that lead to similarities between the twins and derive from family, household, residential area, and the like. Because C is the same for both twins, the correlation is 1. Variance not explained by A or C results from unique environmental factors and measurement error. Because E is unique for both twins, the correlation is 0. We computed twin correlations for Fear and EC to examine whether the within-trait, cross-twin correlations were larger for MZ twins as compared with DZ twins because this would suggest heritability. In addition, we computed partial twin

correlations for Fear and FA with EC as a covariate. In a bivariate twin model, the contribution of A, C, and E factors to the variance in Fear, EC, and FA was examined. In addition, the contribution of A, C, and E to the association between Fear and EC, as well as between Fear and FA, was examined.

Bivariate behavioral genetic analyses were performed with Open Mx (Version 2.7.4) in R (Version 3.3.2) using structural equation modeling. We first used a saturated Cholesky decomposition model to compare with the full bivariate ACE model. We then further tested the ACE model against CE, AE, and E bivariate models, selecting the model with the best goodness of fit. This fit is operationalized as the -2 log likelihood statistic, which is distributed as chi-square ($\chi 2$). The $\chi 2$ test represents the difference in log likelihood between two nested models, with df (degrees of freedom) being the difference in df between the models. When $\chi 2$ is less than 3.84 and shows a p value greater than .05, the more parsimonious model (with fewer parameters) does not significantly deteriorate the fit and, therefore, is preferred. Furthermore, to compare model fit between non-nested models (AE and CE), we used Akaike's information criterion (AIC); better fit is indicated by a lower AIC value. For the model with the best fit, we computed the path loadings. To quantify the relative influence of each of the factors, we first standardized and then squared the path loadings. The correlation within a twin between two traits is represented by the cross-trait, within-twin correlations. When the cross-trait, within-twin correlation was significant, we calculated the extent to which the same genetic or environmental factors influenced both Fear and EC or both Fear and FA, based on the correlations and the standardized path loadings (see Treur, Boomsma, Ligthart, Willemsen, & Vink, 2016).

Results

Twin correlations

Descriptive statistics are summarized in Table 2. A correlation matrix split by zygosity is shown to examine whether the within-trait, cross-twin correlations were larger for MZ twins as compared with DZ twins because this would suggest genetic influence (see Table 2). MZ twins indeed showed higher correlations than DZ twins for Fear and EC but not for FA (Fear: $r_{MZ} = .39$, $p < .01$ and $r_{DZ} = -.06$, $p = .58$; EC: $r_{MZ} = .38$, $p < .01$ and $r_{DZ} = -.26$, $p < .05$; FA: $r_{MZ} = .17$, $p = .16$ and $r_{DZ} = .25$, $p = .12$). The between-trait correlations were significant in MZ twins for EC and FA in Child 1 ($r = -.21$, $p < .05$) but not in Child 2. This means that only in Child 1 of MZ twins is more effortful control related to relatively greater left frontal brain activity. In DZ twins, the correlations between Fear and FA in Child 1 ($r = .30$, $p < .05$) and between Fear in Child 1 and FA in Child 2 ($r = -.29$, $p < .05$) were significant. No other significant correlations were found. Partial twin correlations between Fear and FA, corrected for EC (see Table 2) showed that the correlation between Fear and FA in Child 1 in DZ twins was significant ($r = .36$, $p < .05$). The correlation between Child 1 Fear and Child 2 FA in DZ twins was not significant anymore ($r = -.17$, $p = .31$). No other significant correlations were found between Fear and FA. Therefore, we concluded that EC does not have a large influence on the relation between Fear and FA.

Bivariate ACE model fitting and path loadings

We used two bivariate ACE models to estimate the influence of genetic and shared and unique environmental factors on Fear and EC as well as on Fear and FA. The results of the bivariate models are shown in Table 3. Standardized squared path loadings of each best fitting bivariate model are displayed in Fig. 1. The percentages of A, C, and E explaining variation in Fear may be slightly different among the models because these depend on the specific combination of traits. As a robustness check, univariate models for Fear, FA, and EC are

described in the Appendix A. The cross-trait, within-twin correlation was not significant in any of the bivariate models (Fear and EC: r = -.05; Fear and FA: r = .06); thus, no meaningful analyses of the influence of A, C, or E factors on the overlap between the traits could be performed.

Table 2. Correlations between Fear, EC and FA within and across traits and twins

	Fear C1	Fear C2	EC C1	EC C2	FA C1	FA C2	n	*M*	*SD*
Fear C1	-	-.06	-.16	-.05	**.30***	**-.29***	86	.11	.98
Fear C2	**.39****	-	.01	-.06	-.20	-.04	86	.18	.97
EC C1	-.04	.13	-	**-.26***	-.07	-.12	86	.01	.93
EC C2	-.05	.02	**.38****	-	.08	.09	86	.01	.91
FA C1	.07	-.02	**-.21***	-.13	-	.25	50	-.06	.26
FA C2	-.08	-.01	-.01	-.07	.17	-	58	-.13	.27
n	122	122	122	122	92	88			
M	-.06	-.08	.00	-.06	-.11	-.10			
SD	.84	.82	.88	.88	.23	.22			
Partial correlations between Fear and FA, controlled for EC									
Fear C1					**.36***	-.17			
Fear C2					-.28	-.07			
FA C1	-.01	-.04							
FA C2	-.16	.01							

Note. MZ twins below the diagonal, DZ twins above the diagonal. Sample size, means and standards deviations for MZ twins are presented in the horizontal rows and for DZ twin in vertical rows. Means for Fear and EC are standardized.

*p < .05; ** p < .01

Table 3. Bivariate model fitting of Fear and EC and Fear and FA

	Model	Estimated variables	-2LL	AIC	Compared with	$\Delta \chi^2$	Δdf	*P*
Fear and EC	Saturated model	28	2110.02	502.02	-	-		-
	Full ACE model	11	2149.60	507.60	1	39.58	17	0.001
	AE model	**8**	**2149.60**	**501.60**	**2**	**0.000**	**3**	**1.000**
	CE model	8	2164.04	516.04	2	14.44	3	0.002
	E model	5	2173.42	519.42	3	23.82	3	0.001
Fear and FA	Saturated model	28	1033.74	-318.26	-	-		-
	Full ACE model	11	1065.33	-320.67	1	31.59	17	0.017
	AE model	**8**	**1067.32**	**-324.68**	**2**	**1.99**	**3**	**0.575**
	CE model	8	1071.28	-320.72	2	5.95	3	0.114
	E model	5	1090.48	-307.52	3	25.15	3	0.000

Note: The best fit for each bivariate model is shown in bold. -2LL, difference in likelihood ratio test between the two compared models; AIC, Akaike's information criterion, to compare model fit between the non-nested models AE and CE, a lower value indicates a better fit; Δ χ2, delta chi square, represents the difference in log likelihood between the two compared models using a chi square distribution; Δ df, difference in degrees of freedom between the two compared models

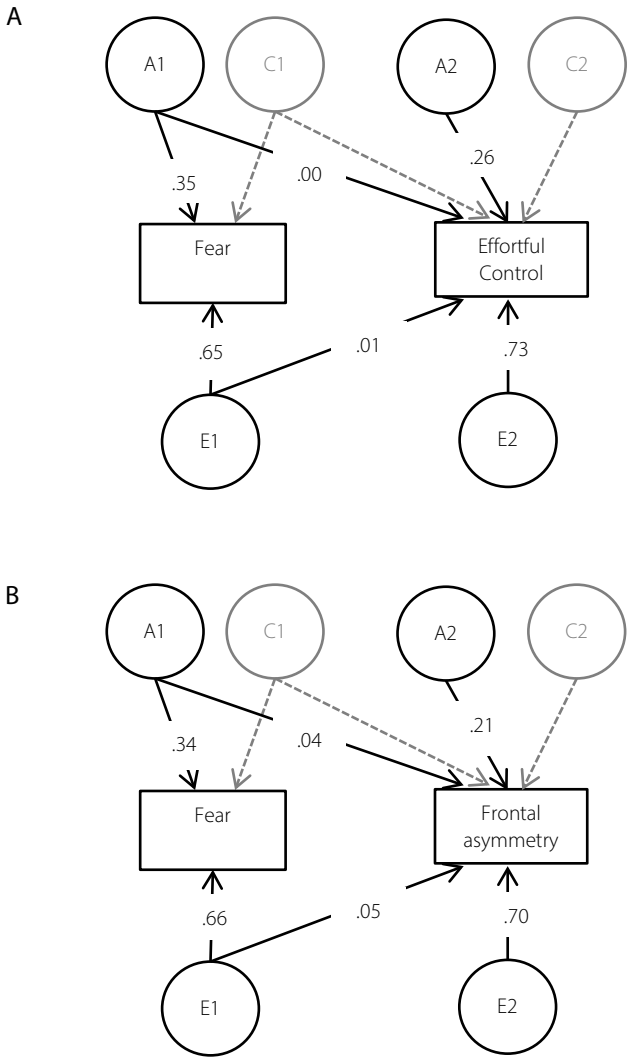

Figure 1. Bivariate twin models with squared path loadings. (A) Fear and EC: AE model, and (B) Fear and FA: AE model. In each model the first factor is explained by the path loadings of A1, C1 and E1 and the second factor is explained by the sum of A1 and A2, C1 and C2 or E1 and E2. Results are shown for the best fitting model, greyed out factors and path loadings were not included.

Fear and EC. The results of the bivariate model with Fear and EC showed that the AE model had the best fit ($\Delta\chi^2 < 3.84$, $p > .05$), indicating that genetic and unique environmental factors account for the variation in Fear and EC. Path loadings of the model (see Fig. 1A) show that individual differences in Fear were explained by genetic factors (35%) and unique environmental factors (65%). Variation in EC was explained by genetic factors (26%) and unique environmental factors (74%).

Fear and FA. The Fear and FA combination also shows that the AE model had the best fit ($\Delta\chi^2 < 3.84$, $p > .05$), indicating that genetic and unique environmental factors account for the variation in Fear and FA. The path loadings (see Fig. 1B) show that individual differences in Fear were explained by genetic factors (34%) and unique environmental factors (66%). Variation in FA was explained by genetic factors (25%) and unique environmental factors (75%).

Discussion

The current study investigated genetic and environmental factors accounting for variation in temperamental traits. We specifically focused on the relation between Fear and EC, as well as between Fear and the possible neural correlate FA, in bivariate behavioral genetic models. Results showed that individual differences in parent-reported Fear and EC, as well as children's FA, were best explained by genetic factors (for about one quarter) and by unique environmental factors (for about three quarters). Cross-trait, within-twin correlations were not significant in any model, precluding overlapping genetic or environmental factors on Fear and EC or on Fear and FA.

In line with previous studies (Anokhin et al., 2006; Clifford et al., 2015; Goldsmith et al., 1997; Lemery-Chalfant et al., 2008; Smit et al., 2007; Van Houtem et al., 2013), we found that Fear and EC and Fear and FA were best explained by genetic and unique environmental factors (AE models). Still, most of the variation between individuals was explained by unique environmental factors. Research conducted with 8-year-old children found a larger influence

of A to explain individual differences in reported Fear and EC (Clifford et al., 2015; Lemery-Chalfant et al., 2008). The twins in our study were on average 3 years younger, so the difference in the ratio of A and E might result from developmental changes. Indeed, a meta-analysis by Kandler and Papendick (2017) showed that the relative contribution of A and E to personality traits changes over the lifespan. However, their results suggest that the influence of genetic factors on personality stability slightly decreases with age, whereas the influence of unique environmental factors increases. Longitudinal studies of the behavioral genetics of Fear, EC, and FA across different age groups are necessary to draw firm conclusions about increases or decreases in A and E.

A potential unique environmental factor influencing Fear, EC, and FA is parenting. Child temperament may elicit certain parenting behaviors, which in turn enhance specific temperamental characteristics (see review in Kiff et al., 2011). With regard to Fear in particular, one study suggested that parental practices such as warmth–reasoning and harshness–hostility are unique environmental factors that influence anxiety in 10- to 18-year-old children (Chen, Yu, & Zhang, 2016). Regarding FA, children who received low-quality maternal caregiving behavior showed relatively greater right FA and more social inhibition at 3 years of age (Hane, Henderson, Reeb-Sutherland, & Fox, 2010). Parenting is often assumed to be a shared environmental factor (i.e. a factor that leads to similarities between the twins), but it can also be a unique environmental factor. For example, although maternal sensitivity is mainly a shared environmental factor influencing infant attachment, attachment security of one twin was also uniquely affected by the relation of the parent with the other twin (Fearon et al., 2006). In addition, twins report that they perceive different parenting (Hannigan, McAdams, Plomin, & Eley, 2016). This indicates that parenting varies between co-twins and may lead to differences between children; as a result, parenting is at least partly a unique environmental factor.

It is important to note that the E factor includes not only unique environmental factors but also measurement error. Recently, a longitudinal cross-cultural study investigating parenting and behavioral and emotional adjustment (based on self-reports) in children (8, 10, and 12 years old) showed that most variation was explained by within-person variability rather than between-person or between-group variability (Deater-Deckard et al., 2018). Accordingly, we believe that measurement error always plays a role when collecting data. However, to minimize measurement error, we used a well-validated instrument that is often used to measure temperament in young children, the CBQ (Putnam & Rothbart, 2006; Rothbart et al., 2001). Our data showed acceptable internal consistency for the subscales Fear and EC. Regarding FA, we observed excellent split-half reliability, suggesting that measurement error is not a factor of great concern. However, some uncertainty regarding the most appropriate quantification of FA in young children remains (see, e.g., Peltola et al., 2014) despite reasonable arguments for the comparability of 6- to 10-Hz activity in young children with adult alpha (Marshall, Bar-Haim, & Fox, 2002).

In addition, the question may arise as to what extent FA reflects a stable trait. In fact, a single measure of resting FA probably reflects a mixture of trait- and state-related variance. Hagemann, Naumann, Thayer, and Bartussek (2002) suggested that 40% of the variance is due to state-related fluctuations (reflecting the participant's response to the recording situation) and 60% is stable trait variance. If genetic factors influence mostly traits, the maximum genetic influence on individual differences in FA can never exceed 60% (Smit et al., 2007) and the presence of state-related variance may help to explain the low A and large E components we obtained. On the other hand, it is possible that MZ twins react more similarly to specific situations, including the laboratory environment and EEG measurement. In that case, not only is the stable trait variance shared between MZ twins but also the state variance should be more similar between MZ twins than between DZ twins. More research is necessary to determine the maximum influence of genetics on FA when using twin models.

With regard to the association between Fear and EC or between Fear and FA, our results showed only few significant cross-trait correlations. Moreover, the bivariate models did not find any significant cross-trait, within-twin correlations, suggesting that the traits were not associated. This is not in line with our hypotheses and previous studies reporting associations between these traits in young children (Cole et al., 2016; Fox et al., 2001; Hill-Soderlund & Braungart-Rieker, 2008; Howarth et al., 2016; Kiff et al., 2011; Rothbart, 2011; Schmidt, 2008). In addition, partial correlations between Fear and FA while controlling for EC were only slightly different from the correlations between Fear and FA without controlling for EC, suggesting that EC did not affect the relation between Fear and FA. One explanation for the lack of associations between the constructs in the current study is that we used trait-related measures rather than settings evoking specific behaviors (such as fearful behavior and right FA during a fear-inducing task). We obtained overall ratings of Fear and EC from parents and FA during a resting EEG measurement because we were specifically interested in individual differences in more stable, task-independent traits. Indeed, other studies using parent-reported Fear and children's resting FA have also failed to find significant relations (Diaz & Bell, 2012; LoBue et al., 2011) or suggest more complex relationships. Howarth et al. (2016), for example, did not find a relation between Fear and FA in 10-month-olds, but they found that parent-reported Fear in 36-montholds predicted right FA when the children were 48 months old. Another possibility is that FA acts like a moderator of temperamental characteristics (cf. Coan & Allen, 2004).

Our study has some limitations that should be addressed in future research. First, about 33% of the children provided no usable FA data (n = 140). However, obtaining EEG measures from young children is challenging, and 40% is a common attrition rate (Bell & Cuevas, 2012). Moreover, the missing FA data is not of great concern for the current study because the behavioral genetic analyses uses FIML modeling that is robust to missing data. Still, sample size remains an important issue. Future studies should aim at including larger samples, for example, by combining studies from several research groups. Second, because of developmental differences and issues relating to the assessment and quantification of both

behavioral and neural indices in 4- to 6-year-olds (including quality and quantity of data and the selection of EEG frequency bands), our results cannot be directly compared with adult studies. Future research should investigate developmental patterns of temperament and FA using measures obtained at several time points from the same individuals. With regard to the reliability of FA, we suggest that future research should determine the optimal number of segments needed to ensure good quality and quantity of EEG measures used for FA computation (see also van Wijk et al., 2017). Third, the generalizability of findings from twin research to singletons is sometimes questioned. However, research has shown that singletons and twins do not differ on temperament (Goldsmith & Campos, 1990) or personality (Johnson, Krueger, Bouchard, & McGue, 2002); therefore, we assume that the individual differences in temperament in early childhood are generalizable from twins to singletons. On the other hand, parents of MZ twins might find it more difficult than parents of DZ twins or singletons to indicate the differences between their children on a temperament questionnaire. This could lead to an overestimation of genetic factors. To overcome this problem, in future studies co-twins could report on their own temperament and on their sibling's temperament, especially in studies with older children. It should be noted that we used Fear and EC ratings from both the primary parent and the other parent to decrease the influence of reporter bias.

In sum, our findings indicate that individual differences in young children's temperament-related traits are best explained by a combination of genetic factors and unique environmental factors. Unique environmental factors in particular accounted for a large proportion of the variance. Exactly which environmental factors are important for temperament development is an important topic for future research given that child temperament is a predictor for success later in life (Zentner & Shiner, 2015). Gaining insight into the specific environmental factors that contribute to temperament will ultimately facilitate support for children who cope with fearfulness or other difficulties with emotion regulation.

References

Anokhin, A. P., Heath, A. C., & Myers, E. (2006). Genetic and environmental influences on frontal EEG asymmetry: A twin study. *Biological Psychology*, 71, 289–295. https://doi.org/10.1016/j.biopsycho.2005.06.004

Bell, M. A., & Cuevas, K. (2012). Using EEG to study cognitive development: Issues and practices. *Journal of Cognitive Development*, 13, 281–294. https://doi.org/10.1080/15248372.2012.691143

Briley, D. A., & Tucker-Drob, E. M. (2014). Genetic and environmental continuity in personality development: A meta-analysis. *Psychological Bulletin*, 140, 1303–1331. https://doi.org/10.1037/a0037091

Buss, A. H., & Plomin, R. (2014). *Temperament: Early developing personality traits* (Vol. 3) New York: Psychology Press. https://doi.org/10.4324/9781315745701

Chen, J., Yu, J., & Zhang, J. (2016). Investigating unique environmental influences of parenting practices on youth anxiety: A monozygotic twin differences study. *International Journal of Behavioral Development*, 40, 205–212. https://doi.org/10.1177/0165025415611261

Clifford, S., Lemery-Chalfant, K., & Goldsmith, H. H. (2015). The unique and shared genetic and environmental contributions to fear, anger, and sadness in childhood. *Child Development, 86*, 1538–1556. https://doi.org/10.1111/cdev.12394

Coan, J. A., & Allen, J. J. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology*, 67, 7–50. https://doi.org/10.1016/j.biopsycho.2004.03.002

Cole, C. E., Zapp, D. J., Fettig, N. B., & Pérez-Edgar, K. (2016). Impact of attention biases to threat and effortful control on individual variations in negative affect and social withdrawal in very young children. *Journal of Experimental Child Psychology*, 141, 210–221. https://doi.org/10.1016/j.jecp.2015.09.012

Coplan, R. J., Prakash, K., O'Neil, K., & Armer, M. (2004). Do you "want" to play? Distinguishing between conflicted shyness and social disinterest in early childhood. *Developmental Psychology*, 40, 244–258. https://doi.org/10.1037/0012-1649.40.2.244

Deater-Deckard, K., Godwin, J., Lansford, J. E., Bacchini, D., Bombi, A. S., Bornstein, M.H., ... Oburu, P. (2018). Within- and between-person and group variance in behavior and beliefs in cross-cultural longitudinal data. *Journal of Adolescence*, 62, 207–217. http://dx.doi.org/10.1016/j.adolescence.2017.06.002

Diaz, A., & Bell, M. A. (2012). Frontal EEG asymmetry and fear reactivity in different contexts at 10 months. *Developmental Psychobiology*, 54, 536–545. https://doi.org/10.1002/dev.20612

Enders, C. K. (2001). A primer on maximum likelihood algorithms available for use with missing data. *Structural Equation Modeling*, 8, 128–141. https://doi.org/10.1207/S15328007SEM0801_7

Euser, S., Bakermans-Kranenburg, M. J., van den Bulk, B. G., Linting, M., Damsteegt, R. C., Vrijhof, C. I., Van Wijk, I.C., Crone, E.A., van IJzendoorn, M. H. (2016). Efficacy of the Video feedback Intervention to Promote Positive Parenting and Sensitive Discipline in Twin Families (VIPP Twins): Study protocol for a randomized controlled trial. *BMC Psychology*, 4(1), 33. https://doi.org/10.1186/s40359-016-0139-y

Fearon, R. M., Van IJzendoorn, M. H., Fonagy, P., Bakermans-Kranenburg, M. J., Schuengel, C., & Bokhorst, C. L. (2006). In search of shared and nonshared environmental factors in security of attachment: A behavior–genetic study of the association between sensitivity and attachment security. *Developmental Psychology*, 42, 1026–1040. http://dx.doi.org/10.1037/0012-1649.42.6.1026

Field, A. P., & Davey, G. C. (2001). Conditioning models of childhood anxiety. In W. K. Silverman & P. D. A. Treffers (Eds.), Anxiety disorders in children and adolescents: Research, assessment and intervention (pp. 187–211). Cambridge, UK: Cambridge University Press.

Fox, N. A., Henderson, H. A., Marshall, P. J., Nichols, K. E., & Ghera, M. M. (2005). Behavioral inhibition: Linking biology and behavior within a developmental framework. *Annual Review of Psychology*, 56, 235–262. https://doi.org/10.1146/annurev.psych.55.090902.141532

Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development*, 72, 1–21. https://doi.org/10.1111/1467-8624.00262

Goldsmith, H. H., Buss, K. A., & Lemery, K. S. (1997). Toddler and childhood temperament: Expanded content, stronger genetic evidence, new evidence for the importance of environment. *Developmental Psychology*, 33, 891–905. https://doi.org/10.1037/0012-1649.33.6.891

Goldsmith, H. H., & Campos, J. J. (1990). The structure of temperamental fear and pleasure in infants: A psychometric perspective. *Child Development*, 61, 1944–1964. https://doi.org/10.2307/1130849

Graham, J. W., Taylor, B. J., Olchowski, A. E., & Cumsille, P. E. (2006). Planned missing data designs in psychological research. *Psychological Methods*, 11, 323–343. https://doi.org/10.1037/1082-989X.11.4.323

Gullone, E. (2000). The development of normal fear: A century of research. Clinical Psychology Review, 20(4), 429–451. https://doi.org/10.1016/S0272-7358(99)00034-3.

Hagemann, D., Naumann, E., Thayer, J. F., & Bartussek, D. (2002). Does resting electroencephalograph asymmetry reflect a trait? An application of latent state–trait theory. *Journal of Personality and Social Psychology*, 82, 619–641. https://doi.org/10.1037/0022-3514.82.4.619

Hane, A. A., Henderson, H. A., Reeb-Sutherland, B. C., & Fox, N. A. (2010). Ordinary variations in human maternal caregiving in infancy and biobehavioral development in early childhood: A follow-up study. *Developmental Psychobiology*, 52, 558–567. https://doi.org/10.1002/dev.20461

Hannigan, L. J., McAdams, T. A., Plomin, R., & Eley, T. C. (2016). Etiological influences on perceptions of parenting: A longitudinal, multi-informant twin study. *Journal of Youth & Adolescence*, 45, 2387–2405. https://doi.org/10.1007/s10964-016-0419-0

Harmon-Jones, E., & Gable, P. A. (2018). On the role of asymmetric frontal cortical activity in approach and withdrawal motivation: An updated review of the evidence. *Psychophysiology*. https://doi.org/10.1111/psyp.12879.

Harmon-Jones, E., Gable, P. A., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology*, 84, 451-462. https://doi.org/10.1016/j.biopsycho.2009.08.010

Henderson, H. A., Marshall, P. J., Fox, N. A., & Rubin, K. H. (2004). Psychophysiological and behavioral evidence for varying forms and functions of nonsocial behavior in preschoolers. *Child Development*, 75, 251–263. https://doi.org/10.1111/j.1467-8624.2004.00667.x

Hill-Soderlund, A. L., & Braungart-Rieker, J. M. (2008). Early individual differences in temperamental reactivity and regulation: Implications for effortful control in early childhood. *Infant Behavior and Development*, 31, 386–397. http://dx.doi.org/10.1016/j.infbeh.2007.12.007

Howarth, G. Z., Fettig, N. B., Curby, T. W., & Bell, M. A. (2016). Frontal electroencephalogram asymmetry and temperament across infancy and early childhood: An exploration of stability and bidirectional relations. *Child Development*, 87, 465–476. https://doi.org/10.1111/cdev.12466

Johnson, W., Krueger, R. F., Bouchard, T. J., & McGue, M. (2002). The personalities of twins: Just ordinary folks. *Twin Research and Human Genetics*, 5, 125–131. https://doi.org/10.1375/twin.5.2.125

Kandler, C., & Papendick, M. (2017). Behavior genetics and personality development: A methodological and meta-analytic review. In J. Specht (Ed.), *Personality development across the lifespan* (pp. 473–495). San Diego: Academic Press. https://doi.org/10.1016/B978-0-12-804674-6.00029-6

Kiff, C. J., Lengua, L. J., & Bush, N. R. (2011). Temperament variation in sensitivity to parenting: Predicting changes in depression and anxiety. *Journal of Abnormal Child Psychology*, 39, 1199–1212. https://doi.org/10.1007/s10802-011-9539-x

Kiff, C. J., Lengua, L. J., & Zalewski, M. (2011). Nature and nurturing: Parenting in the context of child temperament. *Clinical Child and Family Psychology Review*, 14, 251–301. https://doi.org/10.1007/s10567-011-0093-4

Kim, K. J., & Bell, M. A. (2006). Frontal EEG asymmetry and regulation during childhood. *Annals of the New York Academy of Sciences*, 1094, 308–312. https://doi.org/10.1196/annals.1376.040

Kochanska, G., Murray, K. T., & Harlan, E. T. (2000). Effortful control in early childhood: Continuity and change, antecedents, and implications for social development. *Developmental Psychology*, 36, 220–232. https://doi.org/10.1037/0012-1649.36.2.220

Lemery-Chalfant, K., Doelger, L., & Goldsmith, H. H. (2008). Genetic relations between effortful and attentional control and symptoms of psychopathology in middle childhood. *Infant and Child Development*, 17, 365–385. https://doi.org/10.1002/icd.581

Little, T. D., & Rhemtulla, M. (2013). Planned missing data designs for developmental researchers. *Child Development Perspectives*, 7, 199–204. https://doi.org/10.1111/cdep.12043

Little, R. J., & Rubin, D. B. (1989). The analysis of social science data with missing values. *Sociological Methods & Research*, 18, 292–326. https://doi.org/10.1177/0049124189018002004

LoBue, V., Coan, J. A., Thrasher, C., & DeLoache, J. S. (2011). Prefrontal asymmetry and parent rated temperament in infants. *PLoS One*, 6(7) e22694. https://doi.org/10.1371/journal.pone.0022694

Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology*, 113, 1199–1208. https://doi.org/10.1016/S1388-2457(02)00163-3

Mathersul, D., Williams, L. M., Hopkinson, P. J., & Kemp, A. H. (2008). Investigating models of affect: Relationships among EEG alpha asymmetry, depression, and anxiety. *Emotion*, 8, 560-572. https://doi.org/10.1037/a0012811

Neal, L. B., & Gable, P. A. (2017). Regulatory control and impulsivity relate to resting frontal activity. *Social Cognitive and Affective Neuroscience*, 12, 1377–1383. https://doi.org/10.1093/scan/nsx080

Peltola, M. J., Bakermans-Kranenburg, M. J., Alink, L. R., Huffmeijer, R., Biro, S., & van IJzendoorn, M. H. (2014). Resting frontal EEG asymmetry in children: meta-analyses of the effects of psychosocial risk factors and associations with internalizing and externalizing behavior. *Dev. Psychobiol.*, 56(6), 1377–1389. https://doi.org/10.1002/dev.21223.

Putnam, S. P., & Rothbart, M. K. (2006). Development of short and very short forms of the Children's Behavior Questionnaire. *Journal of Personality Assessment*, 87, 102–112. https://doi.org/10.1207/s15327752jpa8701_09

Rietveld, M. J., van der Valk, J. C., Bongers, I. L., Stroet, T. M., Slagboom, P. E., & Boomsma, D. I. (2000). Zygosity diagnosis in young twins by parental report. *Twin Research*, 3(3), 134–141. https://doi.org/10.1375/twin.3.3.134

Rothbart, M. K. (2011). *Becoming who we are: Temperament and personality in development*. New York: Guilford.

Rothbart, M. K., Ahadi, S. A., Hershey, K. L., & Fisher, P. (2001). Investigations of temperament at three to seven years: The Children's Behavior Questionnaire. *Child Development*, 72, 1394-1408. https://doi.org/10.1111/1467-8624.00355

Rothbart, M. K., & Bates, J. E. (2006). Temperament in children's development. In W. Damon, R. Lerner, & N. Eisenberg (Eds.), *Handbook of child psychology, Vol. 3: Social, emotional, and personality development* (6th ed., pp. 99–166). New York: John Wiley.

Rubin, D. B. (1987). *Multiple imputation for nonresponse in surveys*. New York: John Wiley.

Scaini, S., Belotti, R., & Ogliari, A. (2014). Genetic and environmental contributions to social anxiety across different ages: A meta-analytic approach to twin data. *Journal of Anxiety Disorders*, 28, 650–656. https://doi.org/10.1016/j.janxdis.2014.07.002

Schafer, J. L., & Olsen, M. K. (1998). Multiple imputation for multivariate missing-data problems: A data analyst's perspective. *Multivariate Behavioral Research*, 33, 545–571. https://doi.org/10.1207/s15327906mbr3304_5

Schmidt, L. A. (2008). Patterns of second-by-second resting frontal brain (EEG) asymmetry and their relation to heart rate and temperament in 9-month-old human infants. *Personality and Individual Differences*, 44, 216–225. https://doi.org/10.1016/j.paid.2007.08.001

Smit, D. J. A., Posthuma, D., Boomsma, D. I., & De Geus, E. J. C. (2007). The relation between frontal EEG asymmetry and the risk for anxiety and depression. *Biological Psychology*, 74, 26–33. https://doi.org/10.1016/j.biopsycho.2006.06.002

Smith, C. L., Diaz, A., Day, K. L., & Bell, M. A. (2016). Infant frontal electroencephalogram asymmetry and negative emotional reactivity as predictors of toddlerhood effortful control. *Journal of Experimental Child Psychology*, 142, 262–273. https://doi.org/10.1016/j.jecp.2015.09.031

Tabachnick, B. G., & Fidell, L. S. (2006). *Using multivariate statistics*. Boston: Allyn & Bacon.

Thibodeau, R., Jorgensen, R. S., & Kim, S. (2006). Depression, anxiety, and resting frontal EEG asymmetry: A meta-analytic review. *Journal of Abnormal Psychology*, 115, 715–729. https://doi.org/10.1037/0021-843X.115.4.715

Tiberio, S. S., Capaldi, D. M., Kerr, D. C., Bertrand, M., Pears, K. C., & Owen, L. (2016). Parenting and the development of effortful control from early childhood to early adolescence: A transactional developmental model. *Development and Psychopathology*, 28, 837–853. https://doi.org/10.1017/S0954579416000341

Tomarken, A. J., Davidson, R. J., & Henriques, J. B. (1990). Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology*, 59, 791–801. https://doi.org/10.1037/0022-3514.59.4.791

Treur, J. L., Boomsma, D. I., Ligthart, L., Willemsen, G., & Vink, J. M. (2016). Heritability of high sugar consumption through drinks and the genetic correlation with substance use. American *Journal of Clinical Nutrition*, 104, 1144–1150. https://doi.org/10.3945/ajcn.115.127324

Van Houtem, C. M. H. H., Laine, M. L., Boomsma, D. I., Ligthart, L., van Wijk, A. J., & De Jongh, A. (2013). A review and meta-analysis of the heritability of specific phobia subtypes and corresponding fears. *Journal of Anxiety Disorders*, 27, 379–388. https://doi.org/10.1016/j.janxdis.2013.04.007

van Wijk, I. C., van den Bulk, B. G., Euser, S., Bakermans-Kranenburg, M. J., van IJzendoorn, M.H., & Huffmeijer, R. (2017). Social judgments, frontal asymmetry, and aggressive behavior in young children: A replication study using EEG. Neuropsychologia, 126, 120-127. https://doi.org/10.1016/j.neuropsychologia.2017.06.022

Zentner, M., & Shiner, R. L. (Eds.). (2015). *Handbook of temperament*. New York: Guilford.