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Individual differences in dynamic measures of verbal learning abilities in young twin pairs and their older siblings

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ABSTRACT

We explored the genetic background of individual differences in dynamic measures of verbal learning ability in children, using a Dutch version of the Auditory Verbal Learning Test (AVLT). Nine-year-old twin pairs ($N=112$ pairs) were recruited from the Netherlands Twin Register. When possible, an older sibling between 10 and 14 years old participated as well ($N=99$). To assess verbal learning, non-linear curves were fitted for each child individually. Two parameters were estimated: Learning Speed (LS) and Forgetting Speed (FS). Larger twin correlations in monozygotic (MZ) than in dizygotic (DZ) and sibling pairs for LS and FS indicated the importance of genetic factors in explaining variation in these traits. The heritability estimate (percentage of variance explained by genetic factors) for LS was 43% for both twins and siblings. For FS heritability was estimated at 20% in twins and was slightly higher (30%) in their older siblings.

1. Introduction

The ability to store a limited amount of verbal information in highly accessible form over a short period of time, like remembering a shopping list, is an important cognitive ability for both children and adults in everyday life. A specialized component closely linked to these verbal learning abilities, is the phonological loop (Baddeley, Gathercole & Papagno, 1998). The phonological loop can be assessed by the use of verbal repetition paradigms, often called verbal learning paradigms, which may consist of familiar or non-word series of words (Gathercole, Willis, Baddeley & Emslie, 1994). Immediate recall of words is mediated by the semantic similarity between words, word frequency, the order of presentation and is related to long term memory (Cowan, 1988; Burgess & Hitch, 2006; Repovs & Baddeley, 2006; Richardson, 2007).

There are few studies that focus on the etiology of individual differences in verbal learning ability. Learning rates and achievement measures of the ‘same’ process do not necessarily overlap (Byrne et al 2008). This paper focuses on a possible contribution of genetic factors to variation in the dynamics of verbal learning during childhood. The contribution of genetic factors to trait variation can be estimated by comparing the trait similarity between identical (monozygotic, MZ) and non-identical (dizygotic, DZ) twin and sibling pairs. The proportion of the variance in a trait that can be attributed to genetic factors is termed heritability. For general cognitive ability it is well-documented that heritability increases from around 25% in 5- to 6-year olds to 80% in adults (Bartels, Rietveld, van Baal & Boomsma, 2002; Finkel, Pedersen, Plomin & McClearn, 1998; McClearn et al., 1997). Heritability estimates for measures of memory performance also suggest that they differ as a function of age, but data are scarcer than for general cognitive abilities.

Verbal learning is often assessed with the California Verbal Learning Test (CVLT) or the Rey's Auditory Verbal Learning Test (AVLT). The CVLT and AVLT include a list of words that is presented auditorily and repeatedly. Participants have to recall the words immediately after each presentation of the list and after a delay period of 20–30 min. A study in elderly male twin pairs (mean age 71.8 years), showed a heritability of verbal memory of 56 % (Swan et al., 1999). Other word repetition studies with a list of non-words, showed high heritability in young children (Bishop, North & Donlan, 1996; Bishop, Adams & Norbury, 2006; Byrne et al., 2006).

There are a limited number of studies that included a measure of the dynamics during the initial trials of a verbal learning task (e.g. adding and retaining words of a given list into the phonological loop). The most widely used measures of verbal learning are the total number of correctly recalled words or the difference between the correctly recalled words on e.g. trial 5 and trial 1. This is often called the learning slope or learning rate (Woods, Delis, Scott, Kramer &

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Holdnack, 2006; Vakil, Blachstein, Rochberg & Vardi, 2004; Vakil & Blachstein, 1993; Paolo, Troster & Ryan et al., 1997). By taking the difference in recalled words between trials, the learning curve is assumed to be linear while a non-linear learning curve might be more appropriate (van der Elst, Van Boxtel, Van Breukelen & Jolles, 2005; Poreh, 2005; van den Burg & Kingma, 1999). We apply a method to measure the dynamics during the process of keeping words into phonological loop to data collected in a sample of young twins and their siblings. By using non-linear regression analysis and fitting a learning curve for each individual, two parameters are estimated. The first parameter, Learning Speed (LS), represents the proportion of verbal material not yet recalled in a previous trial that is recalled in a following trial. The second parameter, Forgetting Speed (FS), represents the proportion of material that was successfully remembered previously, that can no longer be recalled in a following trial. By estimating these two indices a more comprehensive picture of the dynamics of verbal learning is obtained.

2. Materials and methods

2.1. Participants

Subjects were recruited from the Netherlands Twin Register (Boomsma et al., 2006) and participated in a larger ongoing study, described by van Leeuwen, van den Berg & Boomsma (2008) and Peper et al. (2008) in more detail. A total of 112 healthy twin pairs (23 MZ male, 25 MZ female, 23 DZ male, 21 DZ female, and 20 DZ opposite sex pairs) and their older siblings ($N=99$; 56 female) completed the verbal learning task. Mean age of the twins was 9.1 years, ranging from 8.9 to 9.5 years. Mean age of the siblings was 11.9 years, ranging from 9.9 to 14.9 years. Exclusion criteria consisted of chronic use of medication, any known major medical or psychiatric history, participation in special education or an IQ<70. Socio-economic status (SES) was slightly above the average of the Netherlands (Statistics Netherlands (CBS), 2004), but still showed substantial variation (low SES, $N=17$; middle SES, $N=54$; high SES, $N=37$; unknown SES, $N=4$). Written informed consents were obtained from all subjects and their parents and the study was approved by the Dutch Central Committee on Research involving Human Subjects (CCMO).

2.2. Experimental procedure

The Dutch version of the Rey's Auditory Verbal Learning Test (AVLT) was used (van den Burg & Kingma, 1999). It contains 15 unrelated, concrete nouns and was presented to the children by a neutral computerized voice over 5 identical trials. After each presentation the child was asked to recall as many words as possible.

2.3. Learning and forgetting speed

For each child a non-linear learning curve was fitted using the number of correctly recalled words over the first 5 trials. This learning curve was identified by two parameters, namely Learning Speed (LS) and Forgetting Speed (FS). LS represent the proportion of verbal material not yet recalled in a previous trial that is recalled in a following trial. When LS increase in value, a steeper increase in correctly recalled words is seen over the first 5 trials. FS represents the proportion of material that was successfully remembered previously, that can no longer be recalled in a following trial.

An individual learning curve of the performance from trial 1 to trial 5 was described as: $Y(t)=A*(1-[1-b]^t)$, where Y is the total amount of words recalled, A and b are learning parameters and t is the trial number (Mulder et al., 1996). The formula is derived from the difference equation: $\Delta Y=a-b*Y$, which describes a dynamic growth process. Because the specific task at hand has a fixed amount to be learned, this equation can be reparametrized as: $\Delta Y=a*(15-Y)-b*Y$, where a and b can be interpreted as LS and FS, respectively (in solving this equation it is assumed, that on trial 0 nothing has been learned, that is $Y_{(t=0)}=0$). Both LS and FS were estimated by the Newton–Raphson method for non-linear regression (Dorn & McCracken, 1972).

2.4. Genetic modeling

Structural equation modeling (SEM) was used to decompose variance in LS and FS into genetic and environmental variances (e.g. Boomsma and Molenaar, 1986; Neale, Boker, Xie & Maes, 2006). These estimations are based on the assumption that monozygotic (MZ) twin pairs are genetically identical and share (nearly) 100% of their genetic material, while dizygotic (DZ) twin pairs and full siblings share on average 50% of their segregating genes (Boomsma, Busjahn & Peltonen, 2002). By adding an additional sibling in the analyses statistical power will increase (Posthuma & Boomsma, 2000). Additive genetic effects (A) represent the effects on the phenotype of multiple alleles at different loci on the genome that act additively. It is possible that effects of alleles do not simple add up and depend on the presence of other alleles, resulting in non-additive or dominance genetic effects (D). This results in a relatively large difference between MZ and the DZ correlations. Common environmental influences (C)

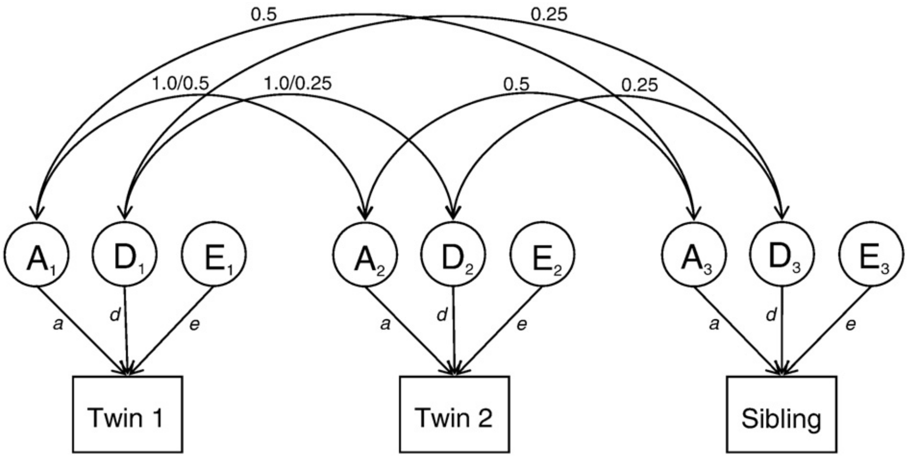

Fig. 1. Genetic ADE model for the LS and FS including the 9-years old twin pairs and their older siblings. Total variance in twins and siblings is explained by A (additive genetic), D (dominance genetic), or E (unique environment) effects. The covariance of the A component between twins (i.e. A_1 and A_2) or twin–sibling pairs is fixed at 1.0 and 0.5 for MZ and DZ, respectively. For twin–sibling pairs (i.e. A_1 and A_3 or A_2 and A_3) the covariance of the A component is fixed at 0.5. Covariance of the D component is fixed at 1.0 and 0.25 for MZ, DZ and twin–sibling pairs respectively. The influence of E is non-shared by family members.

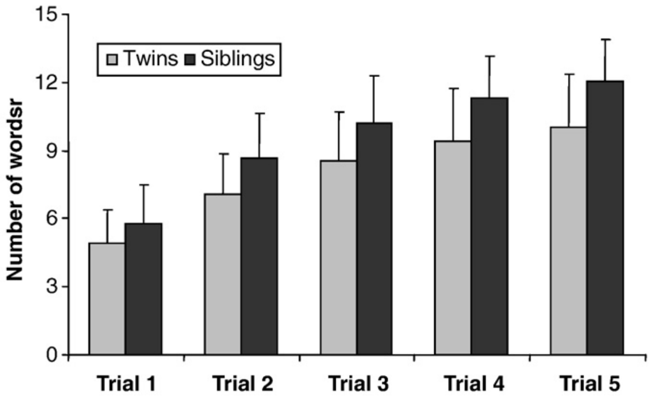

Fig. 2. Mean (± SD) number of correctly recalled words on each trial of the AVLT by the 9-year-old twins and their older siblings.

Table 1
Descriptives for Learning Speed and Forgetting Speed for 9-year-old twins and their older siblings.

	Learning Speed	Forgetting Speed
Mean females	3.28	1.45/0.66[a]
Male deviation	−0.27	n.s.
β age	0.23	n.s.
Variance	0.78	2.57/1.00[a]

Means and variances on Forgetting Speed are given for untransformed data. Further analyses of FS were performed on transformed data.

[a] Significant differences between twins and siblings on mean and variance (twins/sibling).

include all environmental sources of variance that make twins and siblings who grow up within the same family resemble each other. Environmental influences that are unique to an individual and not shared with other family members are referred to as unique environmental influences (E). These also include measurement error (Falconer & Mackay, 1996). The influences of D and C cannot be disentangled when data are collected in twins and siblings raised together. Because we observed MZ correlations more than twice as high as DZ and sibling correlations for both the LS and FS phenotype, an ADE model was fitted to both measures. The ADE model is illustrated in Fig. 1, where the circles represent latent factors (A, D and E) and boxes the measured trait (LS or FS) of the first twin, second twin and sibling.

If A, D and E are standardized to have unit variance, the total variance of a trait due to A, D and E is given by the square of the factor loadings a, d, and e respectively:

$$\mathrm{Var}(P) = a^2 + d^2 + e^2 \tag{1}$$

The correlation between A_1 (the latent genetic factor for twin 1) and A_2 (twin 2) is fixed at 1.0 for MZ twin pairs. The correlation between D_1 and D_2 is also fixed at 1.0 for MZ twin pairs. For DZ twin pairs and twin–sibling pairs, the correlations between A_1, A_2 and D_1, D_2 are 0.5 and 0.25, respectively (Falconer & Mackay, 1996). Unique environmental influences (E) are by definition uncorrelated in all twin and sibling pairs. The covariance between twins and siblings is given by (see also Fig. 1):

$$\text{Covariance MZ twins} = a^2 + d^2 \tag{2}$$

$$\text{Covariance DZ twins and siblings} = 0.5{*}a^2 + 0.25{*}d^2 \tag{3}$$

The software package Mx (Neale et al., 2006) was used to carry out the genetic SEM analyses by fitting Eqs. (1)–(3) to the observed data. In addition, the mean structure of the data was analyzed. In a so-called saturated model (Neale & Cardon, 1992) we compared the means and variances of twins and siblings and of MZ and DZ twins. Twin–twin and twin–sibling correlations and their 95% confidence intervals were estimated for MZ and DZ families. Within this model, regression effects of age and sex on the means were tested for significance. Sex effects on means were explored in two steps. First, sex effects were modeled separately for twins and siblings. Secondly, an overall sex effect was tested for significance.

Next, parameters a, d and e were estimated. All parameters were estimated by maximum likelihood. Models were compared by likelihood ratio tests. By comparing the goodness of fit of nested submodels, where one or more parameters are set at zero or in which parameters are specified to equal other parameters, it is determined which model is the most parsimonious while still describing the data well. The difference in the number of parameters estimated in two nested models gives the degrees of freedom (df). When testing whether a parameter is equal to zero, the likelihood ratio test statistic does not follow a chi-square distribution. The solution is to half the p-values (Dominicus, Skrondal, Gjessing, Pedersen & Palmgren, 2006). Therefore, when testing for the significance of a and d, we report the adjusted p-values.

3. Results

3.1. Phenotypic analyses

Fig. 2 depicts the mean (SD) number of correctly recalled words on each of the first 5 trials. The average number of correctly recalled words increased each following trial for both twins and siblings. LS was normally distributed and FS was positively skewed. After a logarithmic (base 10) transformation the distribution of FS was normal.

Table 1 presents descriptive statistics for LS and FS (for descriptive purposes, untransformed data is presented) based on the learning curves for twins and their siblings.

A significant age effect was found on LS ($\Delta-2\mathrm{LL}=4.02$, $df=1$, $p<0.05$). For FS, no significant age effect was present ($\Delta-2\mathrm{LL}=0.00$, $df=1$, $p=1.00$). Between the 9-year-old twins and their older siblings, the mean value of FS was significantly different ($\Delta-2\mathrm{LL}=20.55$, $df=1$, $p<0.01$). The magnitude of the sex effect was the same in twins and siblings for both parameters (LS $\Delta-2\mathrm{LL}=0.54$, $df=1$, $p=0.46$; FS, $\Delta-2\mathrm{LL}=0.41$, $df=1$, $p=0.52$). Average LS was higher for girls than boys ($\Delta-2\mathrm{LL}=7.64$, $df=1$, $p<0.01$). There was no significant sex effect on FS ($\Delta-2\mathrm{LL}=0.44$, $df=1$, $p=0.51$).

Variances in twins were similar in all sex and zygosity groups for both LS and FS (LS, $\Delta-2\mathrm{LL}=4.24$, $df=5$, $p=0.52$; FS, $\Delta-2\mathrm{LL}=8.21$, $df=5$, $p=0.15$). Also the variance was similar for male and female siblings (LS; $\Delta-2\mathrm{LL}=0.35$, $df=1$, $p=0.55$; FS, $\Delta-2\mathrm{LL}=0.25$, $df=1$, $p=0.62$). Variances were similar in twins and sibling for LS ($\Delta-2\mathrm{LL}=0.00$, $df=1$, $p=0.97$). For FS, the variance in twins was significantly larger than the variance in siblings ($\Delta-2\mathrm{LL}=7.33$, $df=1$, $p<0.01$).

Table 2 presents twin and twin–sibling correlations and their 95% confidence intervals. The statistical power to test for sex effects on covariance structure was low and Table 2 gives MZ, DZ and twin–sib correlations pooled over sexes. The covariance for DZ twin pairs and

Table 2
Twin pair and twin–sibling correlations and their 95% confidence intervals for Learning Speed and Forgetting Speed.

	Learning Speed[a]		Forgetting Speed		
	Correlation	95% CI (*Lower–Upper*)	Correlation	95% CI (*Lower–Upper*)	N
MZ twin pairs	0.49	0.27–0.64	0.41	0.07–0.63	44
DZ twin pairs	0.04	−0.23–0.30	0.07	−0.14–0.28	64
Twin–sibling	0.18	0.03–0.32	0.07	−0.08–0.22	99

[a] Correlation for Learning Speed was corrected for age and sex effects.

Table 3
Results of the ADE model fit on Learning Speed (a) and on Forgetting Speed (b).

a. Learning Speed

Model	A Estimated (Lower/Upper)	D Estimated (Lower/Upper)	E Estimated (Lower/Upper)	Heritability	−2LL	*df*	*p*-value*
1. ADE	0.09 (0.00–0.45)	0.29 (0.00–0.52)	0.40 (0.30–0.55)	0.49	818.649	317	–
2. AE	0.34 (0.20–0.49)	–	0.45 (0.35–0.58)	0.43	819.843	318	$0.14^{(1)}$
3. E	0.79 (0.69–0.90)	–	–	–	839.543	319	$<0.01^{(2)}$

b. Forgetting Speed

Model	A estimated (Lower/Upper)	D estimated (Lower/Upper)	E estimated (Lower/Upper)	T** estimated (Lower/Upper)	Heritability (Twins/Siblings)	−2LL	*df*	*p*-value*
1. ADE(T)**	0.00 (0.00–1.31)	1.58 (0.00–2.68)	1.25 (0.10–2.51)	1.60 (0.62–2.55)	0.36/0.56	1343.780	317	–
2. AE(T)	0.86 (0.15–1.72)	–	1.99 (1.15–2.95)	1.51 (0.53–2.46)	0.20/0.30	1345.663	318	$0.08^{(1)}$
3. E(T)	–	–	2.79 (2.23–3.55)	1.61 (0.63–2.56)	–	1349.786	319	$0.02^{(2)}$

Depicted are the amounts of variance (unstandardized) that can be attributed to Additive genetic (A), Dominance genetic (D), and Unique environment influences (E) and broad heritability estimations (sum of proportions of the total variance that can be attributed to A and D).
*Superscript indicate references model that was used for the likelihood ratio tests.
**Amount of variance includes T component only in the twin group, presenting measurement error. Total variance for siblings does not include the T component.

DZ twin–sibling were similar for both LS ($\Delta -2LL = 0.99$, $df = 1$, $p = 0.32$) and FS ($\Delta -2LL = 0.019$, $df = 1$, $p = 0.89$).

3.2. Genetic modeling

An ADE model, with sex and age as covariates, was fitted to the data on LS. The results are given in Table 3a. A model with the variance due to D constrained at zero did not result in a significant deterioration of model fit ($\Delta -2LL = 1.19$, $df = 1$, $p = 0.14$). Because a model with the variance due to *A* fixed at zero, resulted in a significant detoriation of model fit ($\Delta -2LL = 19.70$, $df = 1$, $p < 0.01$), the AE model is considered to give the best description of the data (see Table 3a). The total variance of LS was 0.79, where 0.34 (43%) was explained by additive genetic effects (A) and 0.45 (57%) explained by unique environment effects (E).

Because means and variances were different between twins and their older siblings for FS, they were allowed to differ in the genetic model for FS. The difference in variances between twins and sibs was modeled by including an additional variance component in twins (T). Total variance for twins was explained by the summation of A, D, E and T, while total variance in siblings remained the summation of A, D, and E. Table 3b contains the results of the model fitting on FS.

When the variance due to D was constrained at zero (i.e. AE(T) model), this did not result in a significantly worse model fit ($\Delta -2LL = 1.88$, $df = 1$, $p = 0.08$). Setting the variance of A at zero, the model showed a significant detoriation in fit ($\Delta -2LL = 4.12$, $df = 1$, $p = 0.02$). Therefore, the AE(T) model was considered as the best fitting model (Table 3b), where 0.86 (20%, and 30% of total variance for twins and siblings, respectively) of the variance could be attributed to additive genetic effects and 1.99 (46% and 70% for twins and siblings, respectively) to unique environmental effects, and 1.51 (35%) for the extra variance in twins only (T).

4. Discussion

To our knowledge this is the first study on the genetic background of individual differences in the dynamics of verbal learning in a population-based sample of unselected young children. Non-linear learning curves were fitted to the data by estimating Learning Speed and Forgetting Speed (LS and FS), giving a more informative view on the dynamics during verbal learning.

Girls had higher LS than boys, while FS did not show any sex differences. LS increased with age, indicating that older children are able to add more new words to their phonological loop while performing the task. This finding is consistent with other studies, (Gathercole, 1999; van den Burg & Kingma, 1999; Forrester & Geffen, 1991; Bishop, Knights & Stoddard, 1990). There was no age effect on FS.

Twin correlations for both LS and FS were higher in MZ twins than in DZ twin pairs and twin–sibling pairs, suggesting genetic influences. LS heritability is estimated at 43%, and FS heritability between 20% and 30%. Because of the relatively small sample size it was not possible to explore sex differences on heritability. Although the differences in correlation between the MZ and the DZ twin pairs to some degree suggested dominance genetic influence (D), this was non-significant for both traits, possibly due to lack of power (Posthuma & Boomsma, 2000).

There was a difference in both mean and variance of the FS parameter between the 9-year old twins and their older siblings, where the mean and variance were larger for the twins. Different explanations are possible for this finding. Differences in means between the two age groups are expected based on the growing literature on a developmental increase in verbal learning. The larger mean scores in twins were accompanied by larger variances. To explore if these larger variances could be attributed to a larger contribution of measurement error in the younger children, we estimated the covariance between DZ twins and between twins and siblings. If the reliable part of the measures is equally associated in these 2 groups, then this argues in favor of the measurement error hypothesis. As the covariances were similar, an extra variance component for twins was included in the genetic model for FS. A larger total variance in young children reduces heritability relative to the older group, because heritability is a ratio (genetic over total variance).

Heritability estimates cannot be higher than the reliability of a test whereas reliability may be higher than heritability. Reliability of the FS and LS measures has to be explored in future research and therefore we do not know to what extent a low reliability might have influenced the present heritability estimates.

Swan et al. (1999) conducted a study in elderly twins, using principal component analysis on different variables derived from the CVLT. The component of verbal learning and memory, which might be of most interest, showed a heritability of 56%. However, this component included both STM and LTM measures, and is therefore difficult to compare to the presented LS and FS, which are representatives of immediate recall. Moreover, this study included elderly twin pairs, and it is known that heritability for general cognitive abilities increases across the life-span (Plomin, DeFries, McClearn & McGuffin, 2001; Bartels et al., 2002).

A similar paradigm, the non-word repetition task, has been used to explore the background of deficits in phonological loop functioning in healthy children (Byrne et al., 2006) and in children with specific language impairments (Gathercole et al., 1994). Deficits in this mechanism have been found to be of genetic origin in young children in the same age range as the present study (Bishop et al., 1996; Bishop et al., 1999; Bishop et al., 2006). Because of methodological differences, it is difficult to compare the heritability estimation between the specific language impairments studies and the present one. In addition to differences in experimental procedures of the two paradigms (i.e. non-word repetition task vs. AVLT paradigm with familiar words), different mechanism can underlie these two sorts of tasks. As a result, it is not unlikely that the magnitude of the genetic influences can differ, or maybe there are different sets of genes involved.

In conclusion, differences in verbal learning abilities are moderately heritable in healthy 9-year-old twin pairs and their older siblings.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.lindif.2009.03.005.

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