Neuroscience and Biobehavioral Reviews 121 (2021) 175–200

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

The heritability of reading and reading-related neurocognitive components: A multi-level meta-analysis

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ARTICLE INFO

Keywords:
Meta-analysis
Reading-related skills
Twin study
Heritability
Genetics

ABSTRACT

Reading ability is a complex task requiring the integration of multiple cognitive and perceptual systems supporting language, visual and orthographic processes, working memory, attention, motor movements, and higher-level comprehension and cognition. Estimates of genetic and environmental influences for some of these reading-related neurocognitive components vary across reports.

By using a multi-level meta-analysis approach, we synthesized the results of behavioral genetic research on reading-related neurocognitive components (i.e. general reading, letter-word knowledge, phonological decoding, reading comprehension, spelling, phonological awareness, rapid automatized naming, and language) of 49 twin studies spanning 4.1–18.5 years of age, with a total sample size of more than 38,000 individuals.

Except for language for which shared environment seems to play a more important role, the causal architecture across most of the reading-related neurocognitive components can be represented by the following equation $a^2 > e^2 > c^2$. Moderators analysis revealed that sex and spoken language did not affect the heritability of any reading-related skills; school grade levels moderated the heritability of general reading, reading comprehension and phonological awareness.

1. Introduction

Reading is a complex, unique ability: it requires the integration of different cognitive skills and it is underlined by extensive brain circuitries. The final outcome of this process is the conversion of arbitrary strings of visual symbols into meaningful sounds. Reading is instrumental to civilization and to daily life and learning, so that reading deficits are a particularly impactful class of childhood and adolescence neurodevelopmental disorders (Peterson and Pennington, 2015).

At the neurocognitive level, reading skills depend on the rapid and accurate integration of a vast circuit of brain areas, the "reading circuit", that subserves: phonology, morphology, syntax, and semantics, as well as visual and orthographic processes, working memory, attention, motor movements, and higher-level comprehension and cognition (Vellutino et al., 2004; Norton and Wolf, 2012; Peterson and Pennington, 2012, 2015). The sophisticated computational procedure of reading acquisition relies therefore upon several reading-related neurocognitive skills. Phonological awareness (PA) refers to the ability to identify and manipulate the sounds of spoken words, which is critical for the establishment and later automatization of letter-sound correspondences. A large amount of evidence supports the relationship between PA and reading skills across languages, with stronger influence in opaque languages (Castles and Coltheart, 2004; Vellutino et al., 2004; Goswami, 2003; Gabrieli, 2009; Peterson and Pennington, 2012). PA contributes to

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https://doi.org/10.1016/j.neubiorev.2020.11.016
Received 8 April 2020; Received in revised form 13 November 2020; Accepted 19 November 2020
Available online 24 November 2020
0149-7634/

mapping speech sounds onto their homologous visual letters, which in turn underlies the attainment of fluent reading (Vellutino et al., 2004). The ability to attend to and maintain phonological units in a phonological memory loop predicts reading abilities (Swanson and Jerman, 2007). Retrieving the meaning of words and comprehending text passages involves multiple memory systems: short-term memory is involved in storing phonological codes, and working memory is involved in maintaining information about words and their meanings as text is integrated to establish coherence and retrieve information from long-term memory (Cain et al., 2004). Working memory is a reliable predictor of reading comprehension (Daneman and Carpenter, 1980) and accounts for a significant proportion of variance in children's reading comprehension ability (Cain et al., 2004). The ability to process auditory stimuli in rapid sequence allows for fine sound-speech discrimination, which is necessary to the adequate acquisition of reading skills (Tallal, 1980, 2004). The ability to rapidly name both linguistic and non-linguistic stimuli maps the processes of connecting and automatizing whole sequences of letters and words with their linguistic information, regardless of writing system (Norton and Wolf, 2012). Notably, reading depends on accurate visual analysis of the stimulus prior to the complex integration of orthographic and phonological information (Vidyasagar, 1999). Visual and auditory attention plays a critical role in the basic letter-to-speech sound integration during letter string processing (Facoetti, 2012; Gori and Facoetti, 2014; Vidyasagar and Pammer, 2010). Before the letter-to-sound mapping mechanism is applied, irrelevant lateral letters should be filtered out by attentional shifting. The perceptual segmentation of the letters string into its constituent graphemes (i.e., graphemic parsing) involves accurate and rapid shifting of spatial and temporal visual attention (Gori and Facoetti, 2014). Thus, visual attention shifting plays a critical role in the basic letter-to-speech sound integration during letter string processing because it is crucially involved in parsing and identification of relevant sub-lexical orthographic units by efficient attentional processing on each letter (Vidyasagar and Pammer, 2010; Facoetti, 2012).

Although the genetics of reading has been investigated by using different approaches (i.e. family studies (Gilger et al., 1994; Schulte-Körne et al., 1996, 2007; Raskind et al., 2000; Hsu et al., 2002; Ziegler et al., 2005), molecular genetic techniques (for a recent review see Mascheretti et al., 2017), GWAS approach (Gialluisi et al., 2014, 2019, 2020; Truong et al., 2019), several studies investigating the etiology of variation in reading-related skills have used the classic twin design (Plomin, 1991; Plomin et al., 2008) and reported significant genetic contributions for reading comprehension, spelling and orthographic coding, as well as for PA, rapid automatized naming (RAN), verbal memory, phonological short-term memory, rapid auditory processing (RAP) and attentional components (i.e., alerting and executive control) (Bishop et al., 1999; Brewer et al., 2016; Byrne et al., 2005, 2007; Olson et al., 2011; Petrill et al., 2006; Plomin and Kovas, 2005). Heritability estimates from these studies using the classical twin model vary widely among (from 0.03 for word reading to 0.83 for phonological awareness) and within (0.03−0.60 for word reading, 0.47−0.72 for word spelling, 0.19−0.83 for PA, 0.60−0.77 for RAN) phenotypes (Gayan and Olson, 2003; Plomin and Kovas, 2005; Byrne et al., 2005, 2007; Olson et al., 2011; Petrill et al., 2006). Similarly, estimates of shared environmental influences and of unique environmental factors vary remarkably (from 0.00 to 0.43 and from 0.04 to 0.38, respectively) across studies (Bates et al., 2004; Byrne et al., 2007; Stevenson et al., 1987; Hohnen and Stevenson, 1999; Stevenson et al., 1987). Meta-analyses of heritability of reading-related skills have been previously conducted (Little et al., 2017; de Zeeuw et al., 2015), but these were focused on reading comprehension (Little et al., 2017) and school achievement (de Zeeuw et al., 2015). Despite the substantial genetic stability, age-to-age genetic correlations were not unity and model fitting results showed significant age-specific as well as school grade-specific genetic influences (Wadsworth et al., 2001, 2007; Harlaar et al., 2007; Astrom et al., 2007; Byrne et al., 2007, 2009; Hayiou-Thomas et al., 2010; Soden et al., 2015; Christopher et al., 2016; Erbeli et al., 2018; Tosto et al., 2017). To our knowledge, however, no meta-analysis systematically examined the effect of moderators such as school grade levels, spoken language, or sex, on heritability estimates. To fill these gaps, and get a better understanding of the contribution of genetic and environmental influences on reading development, we performed a multi-level meta-analysis of twin studies that addressed reading and reading-related neurocognitive phenotypes (such as PA, RAN, spelling and language) underlying reading acquisition and development, and controlled for the effects of school grade levels, sex, and spoken language as moderators.

2. Materials and methods

2.1. Background information: the twin design

All studies included in this meta-analysis employed the classic twin method (Plomin, 1991; Plomin et al., 2008) which is built on the premise that differences in the resemblance between monozygotic twins (sharing approximately 100 % of their DNA) and dizygotic twins (sharing 50 % of their segregating genes on average) can be used to parse phenotypic trait variance into genetic and environmental components. Genetic influences are implied if the correlation between monozygotic twin (MZ) pairs is higher than the correlation between dizygotic twin (DZ) pairs. An influence of the common environment – influences that are shared within the twins– is implied when the DZ twin pair correlation is higher than half of the correlation between MZ twin pairs. Unique environmental factors are person specific and not shared between twins. MZ twin correlation's deviation from 1 provide a direct estimate for the non-shared environmental influences, since identical twins share both their genetic make-up as well as part of the environment (the shared environment). More specifically, twin correlations can be parsed into different components: additive genetic (A), non-additive or dominance genetic (D), shared environmental (C), and non-shared environmental components (E; including measurement error). If MZ correlations are larger than DZ correlations, A, C, and E effects are to be expected. If MZ correlations are more than twice the DZ correlations, non-additive genetic effects are expected. Although in the classical twin design D influences and C influences are confounded and cannot be estimated in the same model, and even if it is common to estimate one or the other based on the twin correlations, this distinction does not influence the results presented in our study as we speak of general genetic influence without specifically modelling the difference between additive or non-additive genetic influences. The classical twin design is based on certain assumptions: (1) the correlation between twins' additive genetic influences is equal to 1.0 for MZ pairs and to 0.5 for DZ pairs, and (2) the correlation between twins' shared environmental influences is equal to 1.0 for both MZ and DZ twin pairs (cf. the equal environments assumption) (Neale and Cardon, 1992; Derks et al., 2006).

2.2. Literature search and selection procedure

The selection of relevant studies started with a research using *twin study*, *reading abilities* and *children* as keywords, and *AND* as Boolean operator to link terms referring to distinct concepts (Salvador-Oliván et al., 2019). As we were interested in several reading-related neurocognitive components, the keyword *reading abilities* was alternately replaced by *phonological awareness, spelling, reading comprehension, rapid naming, phonological short-term memory, visual and auditory attention, visual motion perception, rapid auditory processing*. Research was conduct using two electronic databases, i.e. Medline and PsycINFO, until September 2019. Studies were eligible for this meta-analysis when the following criteria were met:

1) Univariate standardized heritability estimates or twin correlations for at least one reading-related neurocognitive component were available;

2) Sample's age between 5 and 18 years;
3) Sample belonging to the general population;
4) Only papers originally published in English and in peer-reviewed journals.

The initial search in the databases was independently performed by three authors (C.A., R.B., and S.S.) and yielded a total of 318 unique hits. Titles and abstracts of these hits were examined according to the inclusion criteria, resulting in 134 papers that were selected for in-depth reading. We also inspected possible missing publications by screening references of previous published meta-analyses (de Zeeuw et al., 2015; Little et al., 2017), resulting in the identification of 27 additional manuscripts. Subsequently, all 161 articles were screened according to the inclusion criteria, resulting in 49 articles to be included in the present meta-analysis (Fig. 1). The reasons for exclusion were that studies (i) did not provide MZ/DZ correlations or other heritability measures needed to infer the genetic and environmental effects on reading-related skills (57 %), (ii) mentioned the heritability of reading-related neurocognitive traits but did not employ a twin sample (37 %), or (iii) did report twin correlations or heritability estimates for a composite score among different reading measures (7 %).

2.3. Definition of phenotypes

The following phenotypes have been included in further analysis:

1 General Reading: reading speed and accuracy. According to Petrill and colleagues (2007), reading ability can be divided into:

1.1 Letter-word knowledge, i.e. the ability to recognize and identify letters and words (e.g. letter or word identification, word recognition, word reading, reading recognition);

1.2 Phonological decoding, i.e. the ability to correctly relate words with the corresponding verbal sound (e.g. phonological decoding test, irregular word decoding);

1.3 Reading Comprehension, i.e. the ability to semantically comprehend a written text (e.g. passage comprehension, text comprehension, reading achievement);

2 Spelling: the ability to form words with the correct letters in the correct orders (e.g. orthographic decoding, regular and irregular spelling);
3 PA: the ability to recognize and manipulate linguistic sounds apart from their meanings (e.g. rhyming, phoneme isolation, phonemic segmentation, phonemic deletion);
4 RAN: the ability to quickly name aloud objects, pictures, colors, or symbols (letters or digits);
5 Language, such as receptive and expressive vocabulary, oral language and naming abilities.

Although phonological short-term memory, visual and auditory attention, visual motion perception and RAP are crucial reading-related neurocognitive components and have been included as keywords, they were not included in further analysis as too few (< 2) or no studies were available.

2.4. Coding studies

The first authors coded all 49 articles, retrieving descriptive information (authors, article title, journal, year of publication), sample information (country, cohort, sample size, age, sex, spoken language, school grade level), reading-related neurocognitive skills (i.e. general reading, letter-word knowledge, phonological decoding, reading comprehension, PA, RAN, spelling, language), heritability estimates (MZ correlation, DZ correlation, standardized heritability and environment estimates of the overall model if provided and otherwise estimates of the best fitting model). See Table 1 for an overview and description of all the included papers. For every twin correlation, we coded school grade levels[2] (1=preschool/kindergarten; 2=elementary school (Grades 1–5); 3=middle school (Grades 6–8); 4=high school (Grades 9–12)), spoken language (1=English-speaking sample, 2 = non-English-speaking sample), and sex (1=girls, 2=boys).

2.5. Data analyses

The meta-analysis was performed using the 'rma.mv' function of the Metafor package in R version 3.6.1 (Viechtbauer, 2010; Assink and Wibbelink, 2016; R Core Team, 2013). Multiple studies used data from the same cohort resulting in effect sizes from the same sample that were more similar than effect sizes from different studies as they are part of the same sampling process, study group, and study population. Typically, to deal with this dependency, previous meta-analyses only included one eff ;ect size for each sample included study (Bartels, 2015; de Zeeuw et al., 2015; Little et al., 2017). As a result, the statistical power decreases. Multi-level meta-analyses overcome this limitation by taking the dependency among studies into account, while including all eff ;ect sizes (Assink and Wibbelink, 2016; Hendriks et al., 2018; Van den Noortgate et al., 2013).

The analyses were conducted in multiple stages and each step was repeated for all the reading-related neurocognitive phenotypes. As a first step, we meta-analyzed twin correlations (MZ correlation and DZ correlation, respectively), rather than standardized genetic variance. As 14 studies reported only a^2, c^2 and e^2 (Betjemann et al., 2011, 2008; Brooks et al., 1990; Christopher et al., 2013, 2016; Davis et al., 2001; Gayan and Olson, 2003; Harlaar et al., 2007; Hart et al., 2013b; Keenan et al., 2006; Logan et al., 2013; Olson et al., 2011; Petrill and Thompson, 1994; Thompson et al., 1991) and five studies reported only the variance decomposition based on their best fitting model (Bates et al., 2004; Harlaar et al., 2005; van Leeuwen et al., 2009; Malanchini et al., 2017; Taylor and Schatschneider, 2010), we transformed the standardized components into MZ and DZ correlations (Plomin, 2000). Second, both the MZ correlations (r_{MZ}) and the DZ correlations (r_{DZ}) were transformed into the Fisher's Z scores ES_Z (ES_{ZMZ} and ES_{ZDZ}) and the sampling variance for each neurocognitive component was estimated. The Fisher's Z scores are assumed to approach normality, which is necessary for the determination of mean eff ;ect size and for unbiased tests of statistical significance (Lipsey and Wilson, 2001). The sampling variance has been calculated with the following formula: $1/(N\ pairs - 3)$ (Willems et al., 2019). Subsequently, we meta-analyzed the ES_{ZMZ} and the ES_{ZDZ} separately, resulting in an overall ES_{ZMZ} and an overall ES_{ZDZ}. In order to take into account for the dependency between eff ;ect-sizes, we categorized all eff ;ect sizes based on the same sample by coding them with the same "identification number", in line with the multi-level meta-analytic approach (Assink and Wibbelink, 2016; Viechtbauer, 2010). Next, the ES_{ZMZ} and ES_{ZDZ} were transformed back to MZ correlations (r_{MZ}) and DZ correlations (r_{DZ}) for interpretation purposes (Lipsey and Wilson, 2001). We additionally calculated the heritability by applying the Falconer's formula (Falconer, 1960): $h^2 = 2*(r_{MZ} - r_{DZ})$. Third, we examined whether the ES_{ZMZ} and ES_{ZDZ} were potentially moderated by a number of factors such as school grade levels, sex, and spoken language (cf. 'Coding studies' paragraph). As a minimum (at least five) number of studies is recommended to reliably calculate meta-analytic estimates (Borenstein et al., 2011), the effect of school grade levels was investigated for general reading, reading comprehension, and PA; the effect of sex was studied for general reading, and letter-word knowledge; the effect of the spoken language was tested only for general reading (see Supplementary Table 1 for the number of available studies for each moderator upon each neurocognitive component). Specifically, we estimated the Fisher's Z scores ESZ

[2] School grade levels were coded according to the American school system.

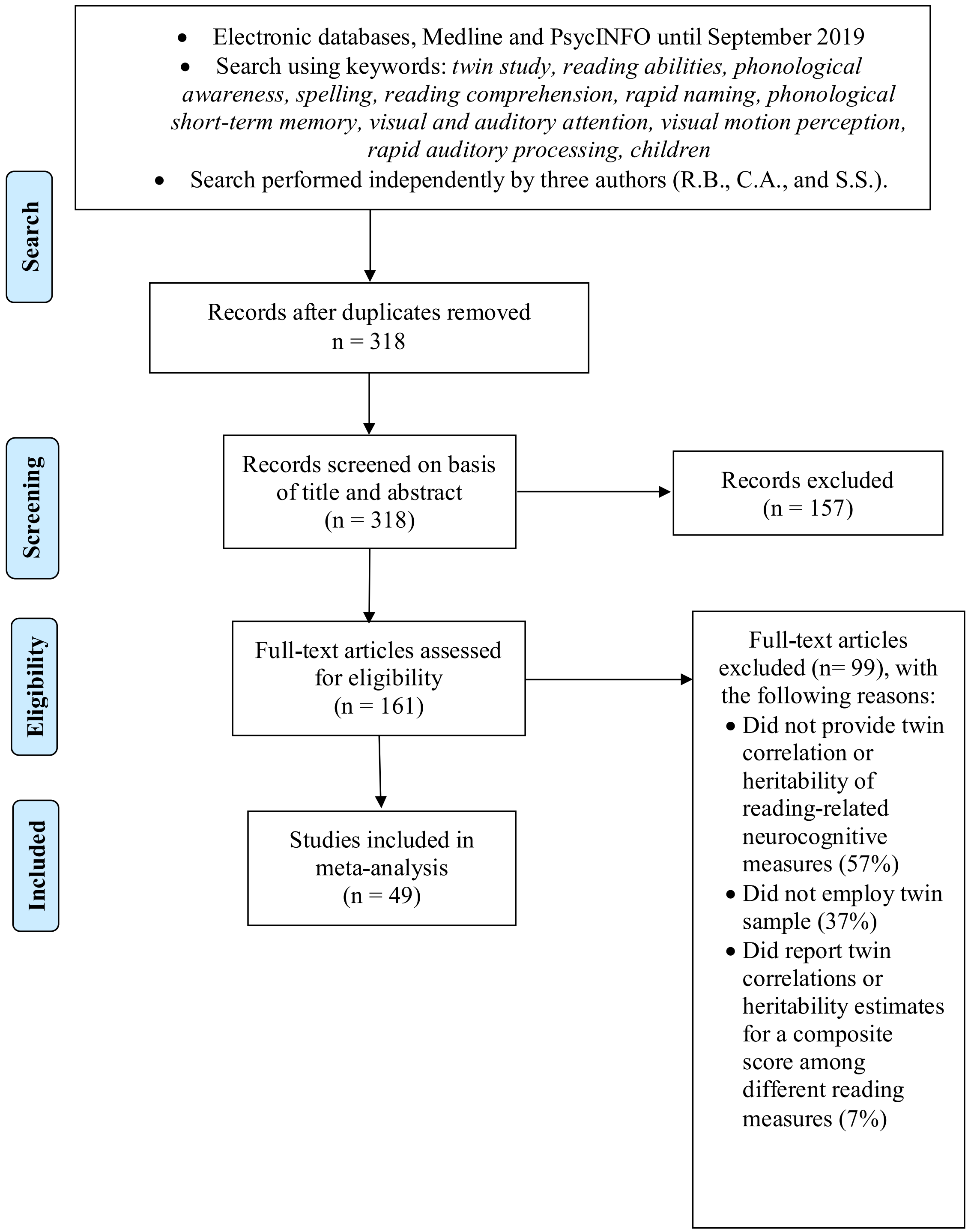

Fig. 1. Flow diagram for the search and inclusion criteria for studies in this meta-analysis. Adapted from Moher at al. (2009).

(ESZMZ and ESZDZ) and the sampling variance for each neurocognitive component within each level of each moderator. Next, the ESZMZ and ESZDZ within each level of each moderator were transformed back to MZ correlations (rMZ) and DZ correlations (rDZ) for interpretation purposes (Lipsey and Wilson, 2001). For each moderator showing a significant effect, we estimated the ratio between the observed correlations within MZ and DZ in order to test whether phenotypic stability could be accounted for by heritable influences (Astrom et al., 2007). Finally, we additionally calculated the heritability within each level of the moderators by applying the Falconer's formula (Falconer, 1960): h2 = 2*(rMZ – rDZ).

3. Results

3.1. Descriptives

A total of 49 articles were included in the analysis (see Table 1 for an overview). Of these 49 articles, 23 papers showed data on independent cohorts. Multiple articles applied data from: The Twins Early Development Study (n = 7), the Colorado Learning Disabilities Research Centre (n = 6), the International Longitudinal Twin Study (n = 5), the Western Reserve Reading Project (n = 4), and the Florida Twin Project on Reading (n = 4). Most studies were conducted on English-speaking

Table 1
Overview of the studies included in meta-analysis.

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
1	Betjemann et al., 2011	USA	CLDRC	Reading comprehension	All	0.92	0.62	0.60 (0.40–0.83)	0.32 (0.10–0.50)	0.08 (0.03–0.15)	8–18 (mean age 11.0)	117	205			1
				Reading comprehension		0.89	0.56	0.66 (0.38–0.87)	0.23 (0.06–0.48)	0.10 (0.03–0.22)	8–18 (mean age 11.0)	117	205			1
				General reading - Letter/Word knowledge		0.93	0.59	0.68 (0.50–0.85)	0.25 (0.09–0.41)	0.07 (0.03–0.13)	8–18 (mean age 11.0)	117	205			1
2	Byrne et al., 2007	USA + Australia	ILTS (USA) & Australian Twin Registry of the National Health and Medical Research Council	Phonological Awareness	All	0.45	0.35	0.19 (0.00–0.54)	0.26 (0.00–0.50)	0.55 (0.41–0.68)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				Phonological Awareness		0.41	0.30	0.29 (0.00–0.57)	0.15 (0.00–0.42)	0.56 (0.42–0.70)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				Rapid Automatized Naming		0.56	0.43	0.56 (0.23–0.82)	0.19 (0.00–0.47)	0.26 (0.18–0.37)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				Rapid Automatized Naming		0.58	0.38	0.56 (0.23–0.82)	0.19 (0.00–0.47)	0.26 (0.18–0.37)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				General reading - Letter/Word knowledge		0.83	0.42	0.81 (0.57–0.87)	0.03 (0.00–0.26)	0.17 (0.13–0.22)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				General reading - Phonological decoding		0.74	0.37	0.71 (0.43–0.79)	0.03 (0.00–0.28)	0.27 (0.21–0.34)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				General reading - Letter/Word knowledge		0.81	0.42	0.81 (0.57–0.87)	0.03 (0.00–0.26)	0.17 (0.13–0.22)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				General reading - Phonological decoding		0.69	0.35	0.71 (0.43–0.79)	0.03 (0.00–0.28)	0.27 (0.21–0.34)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				Reading comprehension		0.77	0.44	0.76 (0.53–0.84)	0.03 (0.00–0.25)	0.21 (0.16–0.27)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
				Spelling		0.77	0.43	0.71 (0.47–0.82)	0.07 (0.00–0.29)	0.22 (0.18–0.29)	7.39 (USA) / 6.99 (Australian)	167	152	2		1
3	Gayan and Olson, 2003	USA	CLDRC	General reading - Letter/Word knowledge	All	0.89	0.47	0.85 (0.69–0.92)	0.04 (0.00–0.19)	0.11 (0.08–0.15)	7.78–18.58 (mean age = 10.56)	257	183			1
				Phonological awareness		0.85	0.45	0.80 (0.62–0.88)	0.05 (0.00–0.21)	0.15 (0.11–0.20)	7.78–18.58 (mean age = 10.56)	257	183			1
				Spelling		0.88	0.45	0.87 (0.75–0.94)	0.01 (0.00–0.11)	0.12 (0.06–0.20)	7.78–18.58 (mean age = 10.56)	257	183			1
				Phonological awareness		0.91	0.50	0.83 (0.62–0.94)	0.08 (0.00–0.27)	0.09 (0.05–0.14)	7.78–18.58 (mean age = 10.56)	257	183			1
4	Byrne et al., 2009	USA	ILTS	General reading - Letter/Word knowledge	All	0.81	0.46	0.82 (0.67–0.88)	0.03 (0.00–0.19)	0.14 (0.12–0.17)	8.40 ± 0.32	185	220	2		1

(*continued on next page*)

Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				Reading Comprehension		0.72	0.45	0.67 (0.50–0.78)	0.07 (0.00–0.23)	0.26 (0.22–0.31)	8.40 ± 0.32	185	220	2		1
				Spelling		0.79	0.41	0.76 (0.64–0.80)	0.00 (0.00–0.11)	0.24 (0.20–0.28)	8.40 ± 0.32	185	220	2		1
				Language		0.85	0.63	0.44 (0.31–0.59)	0.36 (0.22–0.49)	0.19 (0.16–0.23)	8.40 ± 0.32	185	220	2		1
				General reading - Letter/Word knowledge		0.79	0.32				7.80 ± 0.29	86	49	2		1
		Australia	Australian Twin Registry of the National Health and Medical Research Council	Reading Comprehension	All	0.74	0.33				7.80 ± 0.29	86	49	2		1
				Spelling		0.71	0.10				7.80 ± 0.29	86	49	2		1
				Language		0.69	0.54				7.80 ± 0.29	86	49	2		1
				General reading - Letter/Word knowledge		0.84	0.56				8.60 ± 0.31	32	43	2		1
		Scandinavia	Scandinavia	Reading Comprehension	All	0.76	0.46				8.60 ± 0.31	32	43	2		1
				Spelling		0.68	0.24				8.60 ± 0.31	32	43	2		1
				Language		0.84	0.47				8.60 ± 0.31	32	43	2		1
				Rapid Automatized Naming	All	0.45	0.18	0.45	0.00	0.56	8–16 (mean age = 11.11)	224	452			1
5	Christopher et al., 2016	USA	CFR	Rapid Automatized Naming	All	0.49	0.21	0.47	0.00	0.53	8–16 (mean age = 11.11)	224	452			1
				Reading comprehension	All	0.99	0.59	0.82 (0.65–0.99)	0.18 (0.01–0.34)	0.00 (0.00–0.04)	8–16 (mean age = 11.11)	224	452			1
				Phonological awareness		0.67	0.42	0.44 (0.19–0.70)	0.23 (0.08–0.44)	0.33 (0.27–0.42)	6.29 (kindergarten)	265	459	1		1
				Phonological awareness		0.50	0.34	0.44 (0.15–0.67)	0.11 (0.00–0.32)	0.45 (0.37–0.57)	6.29 (kindergarten)	265	459	1		1
6	Erbeli et al., 2018	USA	FTP-R	General reading - Phonological decoding	All	0.59	0.40	0.47 (0.24–0.70)	0.15 (0.00–0.34)	0.38 (0.31–0.46)	7.38 (1 st grade)	265	459	2		1
				General reading - Letter/Word knowledge		0.75	0.49	0.50 (0.37–0.73)	0.22 (0.15–0.33)	0.28 (0.18–0.30)	7.38 (1 st grade)	265	459	2		1
				Reading comprehension		0.74	0.57	0.46 (0.31–0.63)	0.31 (0.16–0.46)	0.23 (0.19–0.27)	13.47 (7th grade)	265	459	3		1
7	Hensler et al., 2010	USA	FTP-R	Reading comprehension	All	0.79	0.53	0.53	0.25	0.21	7.17 ± 0.50	382	642	2		1
				Rapid Automatized Naming		0.74	0.55	0.38 (0.02–0.71)	0.36 (0.07–0.63)	0.25 (0.14–0.40)	6.1–12.17	371	213			1
8	Logan et al., 2013	USA	WRRP	General reading - Letter/Word knowledge	All	0.99	0.91	0.18 (0.04–0.42)	0.82 (0.57–0.96)	0.00 (0.00–0.02)	6.1–12.17	371	213			1
				General reading - Phonological decoding		0.97	0.75	0.45 (0.08–0.97)	0.52 (0.01–0.89)	0.03 (0.00–0.18)	6.1–12.17	371	213			1
						0.89	0.74				6.1–12.17	371	213			1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (hˆ2)	C (cˆ2)	E (eˆ2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
9	Olson et al., 2011	USA + Australia + Scandinavia	ILTS	Reading comprehension	All			0.31 (0.00–0.73)	0.58 (0.22–0.94)	0.06 (0.00–0.23)						
				Rapid Automatized Naming		0.97	0.85	0.25 (0.12–0.38)	0.72 (0.58–0.84)	0.04 (0.01–0.08)	4.10 - 5.00	497	500	1		
				Phonological awareness		0.96	0.83	0.26 (0.16–0.36)	0.70 (0.60–0.78)	0.05 (0.03–0.08)	4.10 - 5.00	497	500	1		
				Language		0.81	0.59	0.45 (0.34–0.58)	0.36 (0.24–0.47)	0.19 (0.16–0.22)	7.11 - 8.90	406	424	2		
				General reading - Letter/Word knowledge		0.86	0.46	0.81 (0.69–0.87)	0.05 (0.00–0.17)	0.14 (0.12–0.17)	7.11 - 8.90	406	424	2		
				General reading - Letter/Word knowledge		0.85	0.46	0.78 (0.65–0.86)	0.07 (0.00–0.19)	0.15 (0.13–0.18)	7.11 - 8.90	406	424	2		
				Reading Comprehension		0.72	0.42	0.61 (0.47–0.73)	0.11 (0.01–0.24)	0.27 (0.24–0.32)	7.11 - 8.90	406	424	2		
		USA	ILTS	Language	All	0.98	0.76	0.44 (0.30–0.63)	0.54 (0.36–0.68)	0.02 (0.00–0.04)	10.50 ± 3.9	176	213	2		1
				General reading - Letter/Word knowledge		0.91	0.53	0.77 (0.57–0.92)	0.14 (0.01–0.34)	0.09 (0.06–0.13)	10.50 ± 3.9	176	213	2		1
				General reading - Letter/Word knowledge		0.87	0.48	0.78 (0.58–0.90)	0.09 (0.00–0.27)	0.14 (0.09–0.19)	10.50 ± 3.9	176	213	2		1
				Reading Comprehension		0.95	0.52	0.86 (0.63–0.95)	0.09 (0.01–0.31)	0.04 (0.01–0.10)	10.50 ± 3.9	176	213	2		1
10	Hohnen and Stevenson, 1999	UK	London area	Language	All	0.80	0.80	0.43	0.35	0.23	5years 8 months-6years 1 month (mean age = 5years 10 months)	32	82	1		1
				Phonological awareness		0.87	0.59	0.52	0.35	0.14	5years 8 months-6years 1 month (mean age = 5years 10 months)	32	82	1		1
				General language		0.90	0.59	0.60	0.39	0.11	6 years 10 months-7 years 4 months (mean age = 7 years)	34	32	2		1
				Phonological awareness		0.92	0.63	0.62	0.28	0.10	6 years 10 months-7 years 4 months (mean age = 7 years)	34	32	2		1
11	Petrill et al., 2007	USA	WRRP	Phonological awareness	All	0.76	0.44	0.59 (0.34–0.78)	0.16 (0.02–0.40)	0.25 (0.19–0.33)	4.9–7.9 (mean age = 6.10)	119	164			1
				Rapid automatized naming		0.58	0.33	0.42 (0.04–0.73)	0.15 (0.0–0.46)	0.44 (0.33–0.62)	4.9–7.9 (mean age = 6.10)	119	164			1
				Language		0.75	0.61					119	164			1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
								0.38 (0.20−0.60)	0.40 (0.19−0.62)	0.22 (0.18−0.28)	4.9–7.9 (mean age = 6.10)					
				General reading - Letter/Word knowledge		0.74	0.55	0.35 (0.14−0.61)	0.38 (0.15−0.61)	0.27 (0.20−0.35)	4.9–7.9 (mean age = 6.10)	119	164			1
				General reading - Letter/Word knowledge		0.87	0.61	0.55 (0.39−0.80)	0.34 (0.11−0.59)	0.11 (0.08−0.15)	4.9–7.9 (mean age = 6.10)	119	164			1
				General reading - Phonological decoding		0.81	0.53	0.56 (0.33−0.81)	0.26 (0.02−0.49)	0.18 (0.14−0.25)	4.9–7.9 (mean age = 6.10)	119	164			1
				Reading comprehension		0.70	0.45	0.50 (0.02−10.0)	0.21 (0.00−0.68)	0.29 (0.19−0.53)	4.9–7.9 (mean age = 6.10)	119	164			1
				Phonological awareness		0.60	0.55	0.14 (0.04−0.39)	0.47 (0.23−0.65)	0.39 (0.31−0.48)	6.0–8.8 (mean age = 7.20)	88	123	2		1
				Rapid automatized naming		0.61	0.38	0.43 (0.07−0.78)	0.20 (0.00−0.51)	0.37 (0.28−0.52)	6.0–8.8 (mean age = 7.20)	88	123	2		1
				Language		0.85	0.62	0.47 (0.30−0.70)	0.40 (0.18−0.64)	0.13 (0.11−0.19)	6.0–8.8 (mean age = 7.20)	88	123	2		1
				General reading - Letter/Word knowledge		0.76	0.63	0.27 (0.10−0.52)	0.52 (0.30−0.79)	0.21 (0.17−0.29)	6.0–8.8 (mean age = 7.20)	88	123	2		1
				General reading - Letter/Word knowledge		0.91	0.59	0.58 (0.41−0.81)	0.33 (0.10−0.57)	0.09 (0.07−0.12)	6.0–8.8 (mean age = 7.20)	88	123	2		1
				General reading - Phonological decoding		0.72	0.44	0.51 (0.22−0.84)	0.21 (0.00−0.49)	0.28 (0.21−0.38)	6.0–8.8 (mean age = 7.20)	88	123	2		1
				Reading comprehension		0.85	0.45	0.76 (0.53−10.0)	0.11 (0.00−0.35)	0.13 (0.10−0.19)	6.0–8.8 (mean age = 7.20)	88	123	2		1
12	Schenker and Petrill, 2015	USA	WRRMP	Reading Comprehension	All	0.75	0.28	0.73 (0.53−0.80)	0.00 (0.00−0.17)	0.27 (0.20−0.37)	From 1 st grade to 7th grade (mean age = 9.81)	116	168			1
				Phonological awareness	All	0.58	0.42	0.37 (0.22−0.51)	0.22 (0.11−0.33)	0.41 (0.35−0.46)	5.53 ± 0.31 (kindergarten)	948	1858	1		1
				Phonological awareness	M	0.58	0.48				5.53 ± 0.31 (kindergarten)	948	1858	1	2	1
				Phonological awareness	F	0.56	0.38				5.53 ± 0.31 (kindergarten)	948	1858	1	1	1
				Phonological awareness	All	0.56	0.38	0.39 (0.07–0.66)	0.18 (0.00–0.42)	0.43 (0.33–0.56)	5.53 ± 0.31 (kindergarten)	112	210	1		1
13	Taylor and Schatschneider, 2010	USA	FSTR	Phonological awareness	All	0.58	0.39	0.43 (0.21–0.64)	0.16 (0.00–0.33)	0.41 (0.33–0.49)	5.53 ± 0.31 (kindergarten)	222	411	1		1
				Phonological awareness	All	0.60	0.49	0.24 (0.00–0.51)	0.37 (0.14–0.57)	0.39 (0.29–0.53)	5.53 ± 0.31 (kindergarten)	101	217	1		1
				Phonological awareness	All	0.68	0.53	0.35 (0.24–0.46)	0.34 (0.25–0.43)	0.31 (0.27–0.35)	5.53 ± 0.31 (kindergarten)	948	1858	1		1
				Phonological awareness	M	0.71	0.50				5.53 ± 0.31 (kindergarten)	948	1858	1	2	1
				Phonological awareness	F	0.64	0.59				5.53 ± 0.31 (kindergarten)	948	1858	1	1	1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				Phonological awareness	All	0.76	0.47	0.54 (0.31–0.78)	0.21 (0.00–0.40)	0.25 (0.19–0.33)	5.53 ± 0.31 (kindergarten)	113	214	1		1
				Phonological awareness	All	0.69	0.54	0.37 (0.21–0.53)	0.34 (0.20–0.47)	0.29 (0.23–0.35)	5.53 ± 0.31 (kindergarten)	228	420	1		1
				Phonological awareness	All	0.52	0.56	0.06 (0.00–0.33)	0.51 (0.30–0.62)	0.43 (0.33–0.53)	5.53 ± 0.31 (kindergarten)	106	221	1		1
				Phonological awareness	All	0.65	0.51	0.26 (0.13–0.38)	0.38 (0.28–0.48)	0.36 (0.32–0.41)	5.53 ± 0.31 (kindergarten)	948	1858	1		1
				Phonological awareness	M	0.62	0.67				5.53 ± 0.31 (kindergarten)	948	1858	1	2	1
				Phonological awareness	F	0.67	0.61				5.53 ± 0.31 (kindergarten)	948	1858	1	1	1
				Phonological awareness	All	0.72	0.45	0.40 (0.14–0.66)	0.28 (0.04–0.48)	0.32 (0.25–0.42)	5.53 ± 0.31 (kindergarten)	110	213	1		1
				Phonological awareness	All	0.54	0.55	0.25 (0.06–0.42)	0.41 (0.27–0.55)	0.34 (0.28–0.42)	5.53 ± 0.31 (kindergarten)	266	411	1		1
				Phonological awareness	All	0.52	0.52	0.01 (0.00–0.30)	0.52 (0.29–0.60)	0.47 (0.36–0.56)	5.53 ± 0.31 (kindergarten)	105	215	1		1
				Phonological awareness	All	0.28	0.39				6.61 ± 0.43 (1 st grade)	886	1684	2		1
				Phonological awareness	M	0.62	0.42				6.61 ± 0.43 (1 st grade)	886	1684	2	2	1
				Phonological awareness	F	0.53	0.32				6.61 ± 0.43 (1 st grade)	886	1684	2	1	1
				Phonological awareness	All	0.69	0.39				6.61 ± 0.43 (1 st grade)	95	203	2		1
				Phonological awareness	All	0.42	0.41				6.61 ± 0.43 (1 st grade)	219	375	2		1
				Phonological awareness	All	0.66	0.39				6.61 ± 0.43 (1 st grade)	102	196	2		1
				General reading - Letter/Word knowledge	All	0.82	0.56	0.62 (0.53–0.72)	0.22 (0.12–0.30)	0.16 (0.14–0.19)	6.61 ± 0.43 (1 st grade)	886	1684	2		1
				General reading - Letter/Word knowledge	M	0.82	0.64				6.61 ± 0.43 (1 st grade)	886	1684	2	2	1
				General reading - Letter/Word knowledge	F	0.83	0.53				6.61 ± 0.43 (1 st grade)	886	1684	2	1	1
				General reading - Letter/Word knowledge	All	0.85	0.58	0.47 (0.28–0.67)	0.36 (0.17–0.52)	0.17 (0.13–0.24)	6.61 ± 0.43 (1 st grade)	95	201	2		1
				General reading - Letter/Word knowledge	All	0.82	0.48	0.74 (0.59–0.86)	0.10 (0.00–0.24)	0.16 (0.13–0.19)	6.61 ± 0.43 (1 st grade)	218	376	2		1
				General reading - Letter/Word knowledge	All	0.78	0.55	0.58 (0.38–0.79)	0.24 (0.04–0.41)	0.18 (0.13–0.25)	6.61 ± 0.43 (1 st grade)	101	195	2		1
14	Tosto et al., 2017	UK	TEDS	General reading - Phonological decoding	All	0.85	0.48	0.73 (0.68−0.78)	0.12 (0.07−0.17)	0.15 (0.14−0.16)	7.16 ± 0.26	1731	3125	2		1
				Language		0.62	0.50	0.27 (0.19−0.35)	0.37 (0.30−0.43)	0.36 (0.34−0.39)	7.16 ± 0.26	1384	2483	2		1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				General reading - Letter/Word knowledge		0.77	0.41	0.71 (0.51–0.76)	0.06 (0.00–0.16)	0.23 (0.02–0.25)	11.72 ± 0.65	1873	3281	3		1
				Reading comprehension		0.62	0.40	0.44 (0.36–0.51)	0.18 (0.12–0.24)	0.38 (0.36–0.41)	11.72 ± 0.65	1858	3278	3		1
				Language		0.68	0.44	0.47 (0.40–0.54)	0.22 (0.15–0.28)	0.31 (0.29–0.34)	11.72 ± 0.65	1600	2747	3		1
				General reading - Letter/Word knowledge		0.67	0.36	0.64 (0.53–0.71)	0.04 (0.00–0.12)	0.32 (0.29–0.35)	16.48 ± 0.27	874	1481	4		1
				Reading comprehension		0.50	0.23	0.51 (0.45–0.55)	0.00 (0.00–0.12)	0.49 (0.45–0.55)	16.48 ± 0.27	730	1202	4		1
				Language		0.62	0.36	0.55 (0.44–0.66)	0.09 (0.00–0.18)	0.36 (0.22–0.39)	16.48 ± 0.27	921	1570	4		1
15	Zumberge et al., 2007	USA	USC	General reading - Letter/Word knowledge	M	0.80	0.50	0.70 (0.54–0.83)	0.11 (0.00–0.26)	0.19 (0.16–0.23)	9.60 ± 0.58	277	328	2	2	1
				General reading - Letter/Word knowledge	F	0.78	0.52				9.60 ± 0.58	277	328	2	1	1
				General reading - Letter/Word knowledge	OS		0.43				9.60 ± 0.58	277	328	2		1
				Phonological awareness	M	0.46	0.37	0.52 (0.43–0.60)	0.00 (0.00–0.00)	0.48 (0.40–0.57)	9.60 ± 0.58	277	328	2	2	1
				Phonological awareness	F	0.54	0.33				9.60 ± 0.58	277	328	2	1	1
				Phonological awareness	OS		0.30				9.60 ± 0.58	277	328	2		1
16	Grasby et al., 2016	Australia	ATR	General reading - Letter/Word knowledge	F	0.75	0.42				8.60 (3rd grade)	262	181	2	1	1
				General reading - Letter/Word knowledge	M	0.75	0.44				8.60 (3rd grade)	245	170	2	2	1
				General reading - Letter/Word knowledge	OS		0.43				8.60 (3rd grade)		303	2		1
				General reading - Letter/Word knowledge	All	0.75	0.43	0.71 (0.58–0.79)	0.05 (0.00–0.17)	0.24 (0.21–0.27)	8.60 (3rd grade)	507	646	2		1
				Spelling	F	0.78	0.45				8.60 (3rd grade)	262	180	2	1	1
				Spelling	M	0.76	0.48				8.60 (3rd grade)	245	163	2	2	1
				Spelling	OS		0.36				8.60 (3rd grade)		305	2		1
				Spelling	All	0.77	0.41	0.76 (0.64–0.81)	0.01 (0.00–0.13)	0.22 (0.19–0.26)	8.60 (3rd grade)	507	648	2		1
				General reading - Letter/Word knowledge	F	0.68	0.54	0.25 (0.04–0.50)	0.43 (0.20–0.61)	0.32 (0.26–0.39)	10.60 (5th grade)	228	166	2	1	1
					M	0.68	0.46					221	170	2	2	1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				General reading - Letter/Word knowledge				0.71 (0.60−0.77)	0.02 (0.00−0.11)	0.27 (0.22−0.33)	10.60 (5th grade)					
				General reading - Letter/Word knowledge	OS		0.30				10.60 (5th grade)		230	2		1
				General reading - Letter/Word knowledge	All	0.68	0.41				10.60 (5th grade)	411	547	2		1
				Spelling	F	0.78	0.40				10.60 (5th grade)	230	166	2	1	1
				Spelling	M	0.76	0.51				10.60 (5th grade)	222	172	2	2	1
				Spelling	OS		0.41				10.60 (5th grade)		281	2		1
				Spelling	All	0.77	0.44	0.77 (0.65−0.83)	0.03 (0.00−0.15)	0.20 (0.17−0.23)	10.60 (5th grade)	452	619	2		1
				General reading - Letter/Word knowledge	F	0.70	0.52				12.50 (7th grade)	210	164	3	1	1
				General reading - Letter/Word knowledge	M	0.72	0.48				12.50 (7th grade)	201	153	3	2	1
				General reading - Letter/Word knowledge	OS		0.38				12.50 (7th grade)		230	3		1
				General reading - Letter/Word knowledge	All	0.71	0.45	0.58 (0.44−0.73)	0.14 (0.00−0.26)	0.28 (0.24−0.32)	12.50 (7th grade)	411	547	3		1
				Spelling	F	0.78	0.44				12.50 (7th grade)	213	163	3	1	1
				Spelling	M	0.74	0.31				12.50 (7th grade)	197	155	3	2	1
				Spelling	OS		0.36				12.50 (7th grade)		223	3		1
				Spelling	All	0.76	0.36	0.78 (0.68−0.81)	0.00 (0.00−0.00)	0.22 (0.19−0.26)	12.50 (7th grade)	410	541	3		1
				General reading - Letter/Word knowledge	F	0.72	0.46	0.61 (0.46−0.77)	0.13 (0.00−0.27)	0.26 (0.22−0.31)	14.50 (9th grade)	195	123	4	1	1
				General reading - Letter/Word knowledge	M	0.73	0.46				14.50 (9th grade)	169	120	4	2	1
				General reading - Letter/Word knowledge	OS		0.43				14.50 (9th grade)		168	4		1
				General reading - Letter/Word knowledge	All	0.72	0.44				14.50 (9th grade)	364	441	4		1
				Spelling	F	0.80	0.39	0.68 (0.48−0.81)	0.12 (0.00−0.31)	0.20 (0.16−0.25)	14.50 (9th grade)	196	125	4	1	1
				Spelling	M	0.73	0.29	0.68 (0.49−0.78)	0.06 (0.00−0.23)	0.26 (0.21−0.33)	14.50 (9th grade)	166	121	4	2	1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				Spelling	OS		0.24				14.50 (9th grade)		166	4		1
				Spelling	All	0.77	0.30				14.50 (9th grade)	362	412	4		1
				Reading Comprehension		0.80	0.52	0.57 (0.37−0.76)	0.24 (0.07−0.41)	0.19 (0.14−0.25)	Grade 1	178	270	2		1
				Reading Comprehension		0.72	0.46	0.52 (0.31−0.71)	0.18 (0.0−0.40)	0.30 (0.24−0.38)	Grade 2	168	238	2		1
				Reading Comprehension		0.80	0.35	0.75 (0.60−0.82)	0.02 (0.0−0.16)	0.22 (0.170.0.29)	Grade 3	171	228	2		1
				Reading Comprehension		0.75	0.33	0.73 (0.55−0.80)	0.02 (0.0−0.20)	0.26 (0.20−0.33)	Grade 4	152	215	2		1
17	Soden et al., 2015	USA	WRRMP	Reading Comprehension	All	0.75	0.27	0.77 (0.520.0.83)	0.0 (0.0−0.23)	0.22 (0.17−0.30)	Grade 5	153	225	2		1
				Reading Comprehension		0.74	0.35	0.74 (0.46−0.81)	0.01 (0.0−0.28)	0.26 (0.19−0.34)	Grade 6	93	150	3		1
				Reading Comprehension		0.78	0.47	0.68 (0.520.0.82)	0.12 (0.0−0.26)	0.20 (0.17−0.24)	Grade 1	440	518	2		1
				Reading Comprehension		0.69	0.46	0.58 (0.41−0.73)	0.14 (0.01−0.29)	0.28 (0.24−0.33)	Grade 2	442	522	2		1
				Reading Comprehension		0.71	0.39	0.70 (0.50−0.76)	0.02 (0.0−0.20)	0.28 (0.23−0.33)	Grade 4	418	510	2		1
				Rapid naming		0.76	0.47	0.58 (0.30−0.83)	0.18 (0.00−0.41)	0.24 (0.16−0.33)	Preschool	224	265	1		1
				Phonological awareness		0.99	0.65	0.71 (0.50−0.97)	0.29 (0.03−0.50)	0.00 (0.00−0.03)	Preschool	224	265	1		1
				Language		0.98	0.87	0.22 (0.05−0.40)	0.76 (0.60−0.91)	0.02 (0.00−0.12)	Preschool	224	265	1		1
				General reading - Letter/Word knowledge		0.85	0.46	0.78 (0.61−0.88)	0.07 (0.00−0.24)	0.14 (0.12−0.18)	Grade 1			2		1
18	Christopher et al., 2015	USA	ILTS	Reading Comprehension	All	0.80	0.46	0.69 (0.51−0.83)	0.11 (0.00−0.28)	0.20 (0.16−0.25)	Grade 1			2		1
				Spelling		0.76	0.43	0.67 (0.48−0.80)	0.09 (0.00−0.27)	0.24 (0.19−0.29)	Grade 1			2		1
				General reading - Letter/Word knowledge		0.73	0.44	0.59 (0.40−0.78)	0.14 (0.00−0.32)	0.26 (0.21−0.33)	Grade 4	213	256	2		1
				Reading Comprehension		0.72	0.36	0.72 (0.51−0.78)	0.00 (0.00−0.19)	0.28 (0.23−0.34)	Grade 4	213	256	2		1
				Spelling		0.83	0.70	0.80 (0.63−0.87)	0.03 (0.00−0.21)	0.16 (0.13−0.20)	Grade 4	213	256	2		1
				General reading - Letter/Word knowledge	M	0.85	0.50	0.68 (0.50–0.86)	0.21 (0.03–0.39)		7.07 ± 0.22	173	132	2	2	1
19	Harlaar et al., 2005	UK	TEDS	General reading - Letter/Word knowledge	F	0.85	0.50	0.50 (0.32–0.68)	0.37 (0.19–0.55)		7.07 ± 0.22	135	114	2	1	1
				General reading - Letter/Word knowledge	OS		0.44				7.07 ± 0.22		228	2		1
20	Malanchini et al., 2017	UK	TEDS	Reading Comprehension	All	0.67	0.47	0.39 (0.30–0.48)	0.28 (0.20–0.35)	0.33 (0.30–0.36)	9 - 10	2502	4425	2		1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				Reading Comprehension		0.35	0.15	0.34 (0.30–0.37)		0.66 (0.63–0.70)	12	2502	4425	3		1
21	Swagerman et al., 2017	Netherlands	NTR	General reading - Letter/Word knowledge	All	0.62	0.26				9 - 21 (mean age = 12.62)	47	70			2
22	Plourde et al., 2015	Quebec	QNTS	General Reading - Phonological Decoding	All	0.52	0.32	0.48 (0.18–0.78)	0.07 (0.21–0.36)	0.45 (0.36–0.54)	5–8 (mean age = 8.11)	218	298			2
				Reading comprehension		0.72	0.32	0.68 (0.44–0.92)	0.03 (0.18–0.25)	0.29 (0.20–0.37)	5–8 (mean age = 8.11)	221	303			2
23	Wong et al., 2014	China - Hong Kong	CTSRD	General reading - Letter/Word knowledge	All	0.90	0.61	0.53 (0.35–0.68)	0.38 (0.19–0.57)	0.09 (0.08–0.10)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Language		0.86	0.80	0.13 (0.02–0.22)	0.74 (0.59–0.87)	0.13 (0.11–0.15)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Phonological awareness		0.67	0.40	0.57 (0.28–0.83)	0.11 (0.14–0.38)	0.32 (0.27–0.36)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Phonological awareness		0.62	0.50	0.36 (0.12–0.60)	0.29 (0.05–0.50)	0.35 (0.30–0.40)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Spelling		0.26	0.16	0.27 (0.07–0.59)	0.01 (0.27–0.30)	0.72 (0.64–0.83)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				General reading - Letter/Word knowledge		0.89	0.52	0.76 (0.53–0.96)	0.14 (0.07–0.37)	0.10 (0.08–0.11)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Language		0.66	0.63	0.11 (0.08–0.30)	0.56 (0.36–0.75)	0.33 (0.28–0.37)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Phonological awareness		0.60	0.61	0.10 (0.11–0.30)	0.52 (0.32–0.72)	0.38 (0.32–0.43)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Phonological awareness		0.74	0.43	0.72 (0.45–0.96)	0.04 (0.02–0.28)	0.24 (0.21–0.28)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
				Spelling		0.33	0.04	0.31 (0.20–0.41)	0.00 (0.00–0.00)	0.69 (0.59–0.78)	3.6–11 (mean age MZ = 6.10; mean age DZ = 6.8)	207	72			2
24	van Leeuwen et al., 2009	Netherlands	NTR		All	0.84	0.40	0.83 (0.74–0.89)			9.1 ± 0.1	106	82	2		2

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				General reading - Letter/Word knowledge												
25	Wing-Yin Chow et al., 2011	Hong Kong	Hong Kong	General reading - Letter/Word knowledge	All	0.90	0.54	0.73 (54–0.92)	0.18 (0.02-0.38)	0.9 (0.08–0.11)	3–11 (mean age = 9.1)	228	84			2
				Language		0.68	0.62	0.11 (-0.60–0.29)	0.57 (0.38–0.75)	0.32 (0.28–0.36)	3–11 (mean age = 9.1)	228	84			2
				Phonological awareness		0.75	0.51	0.50 (0.28–0.71)	0.25 (0.03–0.46)	0.26 (0.22–0.29)	3–11 (mean age = 9.1)	228	84			2
				Phonological awareness		0.71	0.67	0.08 (-0.08–0.23)	0.63 (0.47–0.80)	0.29 (0.25–0.33)	3–11 (mean age = 9.1)	228	84			2
				Rapid Automatized Naming		0.58	0.37	0.42 (-15–0.70)	0.15 (-0.11–0.41)	0.43 (0.37–0.41)	3–11 (mean age = 9.1)	228	84			2
				Spelling		0.55	0.45	0.20 (-0.05–0.45)	0.35 (0.11–0.58)	0.45 (0.40–0.51)	3–11 (mean age = 9.1)	228	84			2
26	Bates et al., 2004	Brisbane area	Brisbane adolescent twin study	General reading - Phonological decoding	F	0.70 (0.55–0.84)	0.43 (0.26–0.59)	0.54	0.17	0.30	18.50 ± 2.7	69	83		1	1
				General reading - Letter/Word knowledge		0.59 (0.41–0.73)	0.33 (0.14–0.50)	0.54	0.07	0.39	18.50 ± 2.7	70	86		1	1
				General reading - Phonological decoding		0.68 (0.54–0.81)	0.26 (0.05–0.45)	0.66	0.03	0.31	18.50 ± 2.7	70	86		1	1
				Spelling		0.73 (0.61–0.85)	0.40 (0.21–0.56)	0.68	0.08	0.24	18.50 ± 2.7	70	86		1	1
				Spelling		0.65 (0.51–0.77)	0.41 (0.23–0.56)	0.52	0.17	0.31	18.50 ± 2.7	70	86		1	1
				Spelling		0.57 (0.40–0.71)	0.19 (0.07–0.41)	0.55	0.00	0.45	18.50 ± 2.7	70	86		1	1
				General reading - Phonological decoding	M	0.72 (0.57–0.85)	0.52 (0.34–0.68)	0.23	0.33	0.27	18.50 ± 2.7	54	83		2	1
				General reading - Letter/Word knowledge		0.56 (0.38–0.71)	0.46 (0.28–0.61)	0.08	0.38	0.41	18.50 ± 2.7	55	86		2	1
				General reading - Phonological decoding		0.69 (0.55–0.82)	0.42 (0.25–0.57)	0.57	0.15	0.28	18.50 ± 2.7	54	86		2	1
				Spelling		0.71 (0.57–0.84)	0.46 (0.27–0.62)	0.53	0.22	0.26	18.50 ± 2.7	53	86		2	1
				Spelling		0.48 (0.28–0.64)	0.38 (0.20–0.54)	0.19	0.31	0.48	18.50 ± 2.7	54	86		2	1
				Spelling		0.45 (0.19–0.64)	0.16 (0.03–0.33)	0.47	0.00	0.53	18.50 ± 2.7	53	86		2	1
				General reading - Phonological decoding	OS		0.41 (0.26–0.55)				18.50 ± 2.7		169			1
				General reading - Letter/Word knowledge			0.26 (0.13–0.39)				18.50 ± 2.7		173			1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				General reading - Phonological decoding			0.38 (0.24–0.51)				18.50 ± 2.7		173			1
				Spelling			0.42 (0.29–0.54)				18.50 ± 2.7		173			1
				Spelling			0.36 (0.24–0.48)				18.50 ± 2.7		173			1
				Spelling			0.28 (0.14–0.42)				18.50 ± 2.7		171			1
				General reading - Letter/Word knowledge		0.77	0.39	0.76 (0.58−0.84)	0.01 (0.00−0.17)	0.23 (0.16−0.34)	8.0–15.9 (mean age = 10.3)	59	57			1
				Reading comprehension		0.71	0.38	0.67 (0.45−0.79)	0.04 (0.00−0.23)	0.29 (0.20−0.42)	8.0–15.9 (mean age = 10.3)	59	57			1
27	Betjemann et al., 2008	USA	CLDRC	General reading - Letter/Word knowledge	All	0.69	0.35	0.68 (0.47−0.78)	0.01 (0.00−0.17)	0.32 (0.22−0.45)	12.9–23.9 (mean age = 15.80)	59	57			1
				Reading comprehension		0.61	0.31	0.60 (0.42−0.72)	0.01 (0.00−0.12)	0.39 (0.28−0.55)	12.9–23.9 (mean age = 15.80)	59	57			1
				General reading - Letter/Word knowledge	All	0.59	0.31				7.9 - 20.4 (mean age = 11.9)	324	263			1
				Reading comprehension	All	0.46	0.31	0.76	0.09	0.15	7.9 - 20.4 (mean age = 11.9)	324	263			1
				Spelling	All	0.62	0.28				7.9 - 20.4 (mean age = 11.9)	324	263			1
28	Davis et al., 2001	USA	CLDRC	Rapid Automatized Naming	All	0.49	0.18				7.9 - 20.4 (mean age = 11.9)	324	263			1
				Rapid Automatized Naming	All	0.54	0.12	0.62	0.03	0.35	7.9 - 20.4 (mean age = 11.9)	324	263			1
				Rapid Automatized Naming	All	0.50	0.26				7.9 - 20.4 (mean age = 11.9)	324	263			1
				Rapid Automatized Naming	All	0.50	0.21				7.9 - 20.4 (mean age = 11.9)	324	263			1
				Reading comprehension	All	0.79	0.47	0.67 (0.62−0.72)	0.11 (0.07−0.16)	0.22 (0.21−0.23)	7	1237	2179	2		1
				Reading comprehension	M	0.77	0.46	0.67 (0.62−0.72)	0.11 (0.07−0.16)	0.22 (0.21−0.23)	7	576	556	2	2	1
29	Harlaar et al., 2007	UK	TEDS	Reading comprehension	F	0.78	0.47	0.67 (0.62−0.72)	0.11 (0.07−0.16)	0.22 (0.21−0.23)	7	661	568	2	1	1
				Reading comprehension	OS		0.41	0.67 (0.62−0.72)	0.11 (0.07−0.16)	0.22 (0.21−0.23)	7		1323	2		1
				Reading comprehension	All	0.75	0.43	0.65 (0.57−0.73)	0.10 (0.03−0.18)	0.25 (0.23−0.27)	9	899	1579	2		1
					M	0.73	0.43				9	411	375	2	2	1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				Reading comprehension				0.65 (0.57–0.73)	0.10 (0.03–0.18)	0.25 (0.23–0.27)						
				Reading comprehension	F	0.77	0.41	0.65 (0.57–0.73)	0.10 (0.03–0.18)	0.25 (0.23–0.27)	9	488	429	2	1	1
				Reading comprehension	OS		0.43	0.65 (0.57–0.73)	0.10 (0.03–0.18)	0.25 (0.23–0.27)	9		1323	2		1
				Reading comprehension	All	0.75	0.48	0.57 (0.49–0.65)	0.17 (0.11–0.24)	0.26 (0.23–0.28)	10	921	1651	2		1
				Reading comprehension	M	0.73	0.53	0.57 (0.49–0.65)	0.17 (0.11–0.24)	0.26 (0.23–0.28)	10	406	394	2	2	1
				Reading comprehension	F	0.74	0.45	0.57 (0.49–0.65)	0.17 (0.11–0.24)	0.26 (0.23–0.28)	10	515	437	2	1	1
				Reading comprehension	OS		0.41	0.57 (0.49–0.65)	0.17 (0.11–0.24)	0.26 (0.23–0.28)	10		1323	2		1
				General reading - Phonological decoding		0.82 (0.74–0.88)	0.43 (0.28–0.57)	0.73 (0.55–0.84)	0.11 (0.00–0.28)	0.16 (0.12–0.21)	9.86 ± 0.89	88	130	2		1
				General reading - Phonological decoding		0.79 (0.70–0.86)	0.43 (0.27–0.56)	0.71 (0.47–0.84)	0.10 (0.00–0.30)	0.19 (0.15–0.26)	9.86 ± 0.89	84	127	2		1
				General reading - Letter/Word knowledge		0.82 (0.74–0.88)	0.43 (0.28–0.57)	0.81 (0.55–0.88)	0.03 (0.00–0.27)	0.17 (0.12–0.23)	9.86 ± 0.89	88	129	2		1
30	Harlaar et al., 2010	USA	WRRP	General reading - Letter/Word knowledge	All	0.73 (0.61–0.82)	0.32 (0.16–0.47)	0.78 (0.61–0.84)	0.00 (0.00–0.14)	0.22 (0.16–0.31)	9.86 ± 0.89	88	130	2		1
				Language		0.80 (0.72–0.87)	0.61 (0.49–0.71)	0.49 (0.29–0.71)	0.35 (0.14–0.52)	0.16 (0.12–0.22)	9.86 ± 0.89	88	131	2		1
				Language		0.56 (0.39–0.69)	0.49 (0.34–0.61)	0.24 (0.07–0.51)	0.34 (0.12–0.51)	0.42 (0.32–0.52)	9.86 ± 0.89	87	127	2		1
				Reading Comprehension		0.73 (0.61–0.82)	0.25 (0.07–0.42)	0.75 (0.57–0.83)	0.00 (0.00–0.00)	0.25 (0.17–0.36)	9.86 ± 0.89	81	121	2		1
				Reading Comprehension		0.60 (0.44–0.72)	0.23 (0.06–0.38)	0.58 (0.30–0.69)	0.00 (0.00–0.00)	0.42 (0.31–0.56)	9.86 ± 0.89	87	129	2		1
31	Hart et al., 2013a	USA	FTPRBE	Reading Comprehension	All	0.83	0.53	0.67 (0.52–0.83)	0.17 (0.02–0.18)	0.15 (0.12–0.18)	8.18 ± 1.33	189	388	2		1
				General reading - Letter/Word knowledge	M	0.79	0.44	0.72	0.10	0.18	11.19 ± 2.54	292	179		2	1
32	Reynolds et al., 1996	USA	VTSABD	General reading - Letter/Word knowledge	F	0.81	0.52	0.59	0.22	0.19	11.19 ± 2.54	380	184		1	1
				General reading - Letter/Word knowledge	OS		0.39				11.19 ± 2.54		284			1
				General reading - Letter/Word knowledge		0.82	0.57				8.5 - 10.8 (mean age = 9.6)	13	22	2		1
33	Lytton et al., 1988	Canada (Calgary)		Reading comprehension	All	0.55	0.44				8.5 - 10.8 (mean age = 9.6)	13	22	2		1
				Spelling		0.81	0.24					13	22	2		1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
											8.5 - 10.8 (mean age = 9.6)					
34	Stevenson et al., 1987	UK	London sample	General reading - Letter/Word knowledge	All	0.62	0.53	0.18	0.44	0.31	13	194	356	3		1
				Reading comprehension		0.71	0.49	0.44	0.27	0.15	13	194	356	3		1
				General reading - Letter/Word knowledge		0.61	0.51	0.19	0.42	0.34	13	190	354	3		1
				Spelling		0.76	0.50	0.53	0.23	0.30	13	192	353	3		1
35	Olson et al., 2013	USA	CLDRC	Phonological Awareness	All	0.80	0.39	0.79 (0.60–0.85)	0.00 (0.00–0.17)	0.21 (0.15–0.29)	8–18 (mean age = 12)	81	189			1
				Rapid Automatized Naming		0.73	0.25	0.70 (0.54–0.79)	0.00 (0.00–0.11)	0.30 (0.21–0.42)	8–18 (mean age = 12)	81	189			1
				Language		0.89	0.64	0.51 (0.35–0.69)	0.38 (0.20–0.53)	0.11 (0.08–0.16)	8–18 (mean age = 12)	81	189			1
				General reading - Letter/Word knowledge		0.91	0.50	0.81 (0.62–0.93)	0.09 (0.00–0.28)	0.10 (0.07–0.14)	8–18 (mean age = 12)	81	189			1
				Spelling		0.91	0.48	0.87 (0.67–0.93)	0.03 (0.00–0.23)	0.09 (0.07–0.13)	8–18 (mean age = 12)	81	189			1
				Reading Comprehension		0.88	0.49	0.83 (0.63–0.92)	0.05 (0.00–0.25)	0.12 (0.08–0.16)	8–18 (mean age = 12)	81	189			1
36	Byrne et al., 2013	USA + Australia + Scandinavia	CTR & ATR & Medical Birth Registries in Norway and Sweden.	RAN	All	0.76	0.62	0.23 (0.12–0.34)	0.52 (0.42–0.61)	0.25 (0.22–0.29)	Grade 1	520	522	2		1
				Language		0.58	0.51	0.16 (0.01–0.31)	0.42 (0.29–0.54)	0.42 (0.37–0.47)	Grade 1	520	522	2		1
				Language		0.82	0.59	0.45 (0.34–0.57)	0.37 (0.25–0.57)	0.19 (0.16–0.22)	Grade 2	443	437	2		1
				General reading - Letter/Word knowledge		0.76	0.68	0.18 (0.09–0.28)	0.58 (0.49–0.66)	0.23 (0.20–0.27)	Grade 1	520	522	2		1
				General reading - Phonological decoding		0.81	0.43	0.83 (0.70–0.85)	0.00 (0.00–0.13)	0.17 (0.15–0.20)	Grade 2	443	437	2		1
				General reading - Phonological decoding		0.80	0.43	0.81 (0.67–0.85)	0.01 (.000–0.14)	0.18 (0.15–0.21)	Grade 2	443	437	2		1
37	Hart et al., 2009a,2009b	USA	WRRP	RAN	All	0.71	0.33	0.72 (0.42–0.88)	0.00 (0.00–0.27)	0.29 (0.22–0.39)	4.33–8.25 (mean age = 6.09)	128	175			1
				RAN		0.56	0.43	0.79 (0.52–0.96)	0.00 (0.00–0.00)	0.22 (0.17–0.31)	6.00–8.83 (mean age = 7.16)	128	175	2		1
				RAN		0.68	0.27	0.65 (0.49–0.83)	0.00 (0.00–0.00)	0.32 (0.24–0.44)	6.92–10.00 (mean age = 8.32)	128	175	2		1
				RAN		0.54	0.42	0.42 (0.00–0.82)	0.17 (0.00–0.55)	0.39 (0.28–0.59)	8.01–12.13 (mean age = 9.89)	128	175			1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				General Reading		0.82	0.50	0.45 (0.11–0.87)	0.28 (0.00–0.65)	0.19 (0.13–0.30)	4.33–8.25 (mean age = 6.09)	128	175			1
				General Reading		0.86	0.44	0.76 (0.52–0.98)	0.07 (0.00–0.33)	0.15 (0.11–0.20)	6.00–8.83 (mean age = 7.16)	128	175	2		1
				General Reading		0.77	0.40	0.81 (0.56–1.00)	0.00 (0.00–0.00)	0.17 (0.12–0.24)	6.92–10.00 (mean age = 8.32)	128	175	2		1
				General Reading		0.85	0.29	0.94 (0.72–1.20)	0.00 (0.00–0.00)	0.12 (0.08–0.18)	8.01–12.13 (mean age = 9.89)	128	175			1
38	Hart et al., 2013b	USA	FTP-R	General Reading	SS	0.82	0.47	0.85 (0.75–0.94)	0.01 (0.00–0.12)	0.14 (0.13–0.16)	Grade 1	486	468	2		1
				General Reading	OS		0.45	0.85 (0.75–0.94)	0.01 (0.00–0.12)	0.14 (0.13–0.16)	Grade 1		442	2		1
				General Reading	SS	0.85	0.59	0.63 (0.54–0.73)	0.22 (0.12–0.32)	0.15 (0.13–0.17)	Grade 2	447	417	2		1
				General Reading	OS		0.48	0.63 (0.54–0.73)	0.22 (0.12–0.32)	0.15 (0.13–0.17)	Grade 2		406	2		1
				General Reading	SS	0.85	0.60	0.56 (0.45–0.67)	0.28 (0.16–0.40)	0.16 (0.13–0.18)	Grade 3	303	295	2		1
				General Reading	OS		0.51	0.56 (0.45–0.67)	0.28 (0.16–0.40)	0.16 (0.13–0.18)	Grade 3		298	2		1
				General Reading	SS	0.82	0.52	0.65 (0.42–0.89)	0.16 (0.00–0.39)	0.19 (0.14–0.25)	Grade 4	108	83	2		1
				General Reading	OS		0.45	0.65 (0.42–0.89)	0.16 (0.00–0.39)	0.19 (0.14–0.25)	Grade 4		96	2		1
				General Reading	SS	0.73	0.30	0.71 (0.35–1.01)	0.09 (0.00–0.42)	0.20 (0.14–0.33)	Grade 5	48	42	2		1
				General Reading	OS		0.48	0.71 (0.35–1.01)	0.09 (0.00–0.42)	0.20 (0.14–0.33)	Grade 5		44	2		1
39	Harlaar et al., 2012	UK	TEDS	General Reading	All	0.77 (0.74–0.79)	0.39 (0.36–0.42)	0.74 (0.68–0.76)	0.02 (0.01–0.08)	0.24 (0.22–0.25)	11–12 (mean age = 11.87)	1511	2603	3		1
				General reading - Letter/Word knowledge		0.72 (0.70–0.74)	0.41 (0.38–0.44)	0.64 (0.59–0.70)	0.08 (0.03–0.13)	0.28 (0.26–0.30)	11–12 (mean age = 11.87)	1702	2978	3		1
				Reading Comprehension		0.46 (0.42–0.50)	0.30 (0.27–0.33)	0.34 (0.27–0.42)	0.13 (0.04–0.19)	0.53 (0.50–0.56)	11–12 (mean age = 11.87)	1715	3057	3		1
				Reading Comprehension		0.56 (0.52–0.59)	0.37 (0.33–0.40)	0.37 (0.30–0.44)	0.18 (0.13–0.24)	0.45 (0.42–0.47)	11–12 (mean age = 11.87)	1748	3117	3		1
40	Thompson et al., 1991	USA	WRTP	General Reading	All	0.93	0.795	0.27	0.66	0.07	6 - 12 (mean age = 9.80)	146	132			1
				Language		0.84	0.745	0.19	0.65	0.16	6 - 12 (mean age = 9.80)	146	132			1
41	Books et al., 1990	USA	Colorado Twin Study of Reading Disability	General reading - Letter/Word knowledge	All	0.52	0.295	0.45	0.07	0.48	7.8 - 20.6 (mean age = 12.6)	86	60			1
				Reading Comprehension		0.46	0.325	0.27	0.19	0.36	7.8 - 20.6 (mean age = 12.6)	86	60			1
				Spelling		1.00	0.45	0.48	0.53	0.43		86	60			1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
											7.8 - 20.6 (mean age = 12.6)					
42	Christopher et al., 2013	USA + Australia + Scandina	ILTS	General reading - Letter/Word knowledge	All	0.9	0.56	0.68 (0.54–0.85)	0.22 (0.05–0.36)	0.10 (0.08–0.12)	5.50–7.08 (mean age = 6.27)	225	262			1
				General reading - Letter/Word knowledge		0.86	0.44	0.84 (0.66–0.89)	0.02 (0.00–0.20)	0.14 (0.11–0.17)	6.58–8.67 (mean age = 7.42)	225	262	2		1
				General reading - Letter/Word knowledge		0.81	0.445	0.73 (0.56, 0.84)	0.08 (0.00–0.24)	0.19 (0.15–0.23)	7.67–9.50 (mean age = 8.45)	225	262	2		1
				General reading - Letter/Word knowledge		0.72	0.435	0.57 (0.36–0.76)	0.15 (0.00–0.32)	0.29 (0.23–0.36)	9.67–11.67 (mean age = 10.45)	210	254	2		1
				General reading - Phonological decoding		0.75	0.435	0.63 (0.43–0.79)	0.12 (0.00–0.30)	0.25 (0.21–0.31)	5.50–7.08 (mean age = 6.27)	225	262			1
				General reading - Phonological decoding		0.82	0.41	0.82 (0.70–0.85)	0.00 (0.00–0.11)	0.18 (0.15–0.22)	6.58–8.67 (mean age = 7.42)	225	262	2		1
				General reading - Phonological decoding		0.79	0.415	0.75 (0.56–0.83)	0.04 (0.00–0.22)	0.21 (0.17–0.26)	7.67–9.50 (mean age = 8.45)	225	262	2		1
				General reading - Phonological decoding		0.77	0.4	0.74 (0.55–0.82)	0.03 (0.00–0.22)	0.22 (0.18–0.28)	9.67–11.67 (mean age = 10.45)	210	254	2		1
				Reading Comprehension		0.81	0.455	0.71 (0.53–0.83)	0.10 (0.00–0.26)	0.20 (0.16–0.25)	6.58–8.67 (mean age = 7.42)	225	262	2		1
				Reading Comprehension		0.73	0.435	0.59 (0.39–0.77)	0.14 (0.00–0.31)	0.27 (0.22–0.34)	7.67–9.50 (mean age = 8.45)	225	262	2		1
				Reading Comprehension		0.72	0.38	0.68 (0.47–0.77)	0.04 (0.00–0.23)	0.28 (0.23–0.35)	9.67–11.67 (mean age = 10.45)	210	254	2		1
				Spelling		0.78	0.44	0.68 (0.49–0.81)	0.10 (0.00–0.27)	0.23 (0.19–0.28)	6.58–8.67 (mean age = 7.42)	225	262	2		1
				Spelling		0.81	0.405	0.81 (0.62–0.85)	0.00 (0.00–0.18)	0.19 (0.15–0.23)	7.67–9.50 (mean age = 8.45)	225	262	2		1
				Spelling		0.84	0.455	0.77 (0.59–0.87)	0.07 (0.00–0.24)	0.16 (0.13–0.20)	9.67–11.67 (mean age = 10.45)	210	254	2		1
43	Davis et al., 2008	UK	TEDS	Reading Comprehension	All	0.64 (0.60–0.67)	0.43 (0.39–0.47)				10	919	1622	2		1
				Reading Comprehension	M	0.64 (0.58–0.70)	0.43 (0.34–0.51)				10	383	373	2	2	1
				Reading Comprehension	F	0.63 (0.58–0.68)	0.46 (0.38–0.53)				10	536	444	2	1	1
44	Davis et al., 2009	UK	TEDS		All	0.72 (0.70–0.75)	0.42 (0.38–0.45)				12	1667	2844	3		1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				General reading - Letter/Word knowledge												
				Reading Comprehension		0.55 (0.52–0.58)	0.35 (0.31–0.38)				12	1694	2950	3		1
				Reading Comprehension		0.49 (0.45–0.52)	0.32 (0.29–0.35)				12	1635	2812	3		1
				General reading		0.75 (0.73–0.77)	0.38 (0.35–0.41)				12	1488	2540	3		1
				Language		0.44 (0.40–0.48)	0.29 (0.25–0.33)				12	1377	2312	3		1
45	Harris, 1982	USA	Indiana University Twin Panel	General reading - Letter/Word knowledge	All	0.787	0.460				6.71 - 9.26 (mean age = 7.73)	57	31	2		1
				General reading - Letter/Word knowledge		0.914	0.636				6.71 - 9.26 (mean age = 7.73)	57	31	2		1
				General reading - Phonological decoding		0.870	0.365				6.71 - 9.26 (mean age = 7.73)	57	31	2		1
				Reading Comprehension		0.804	0.662				6.71 - 9.26 (mean age = 7.73)	57	31	2		1
				Reading Comprehension		0.786	0.623				6.71 - 9.26 (mean age = 7.73)	57	31	2		1
46	Hart et al., 2010b	USA	WRRMP	General reading - Phonological decoding	All	0.74	0.37	0.74 (0.52–0.92)	0.00 (0.00–0.00)	0.27 (0.20–0.37)	7.4–12.3 (mean age = 9.86)	94	134			1
				General reading - Letter/Word knowledge		0.83	0.43	0.80 (0.54–1.00)	0.03 (0.00–0.29)	0.17 (0.13–0.23)	7.4–12.3 (mean age = 9.86)	94	134			1
				General reading		0.84	0.42	0.84 (0.63–1.02)	0.00 (0.00–0.00)	0.17 (0.13–0.24)	7.4–12.3 (mean age = 9.86)	94	134			1
				General reading - Letter/Word knowledge		0.82	0.41	0.82 (0.58–.99)	0.00 (0.00–0.23)	0.17 (0.13–0.23)	7.4–12.3 (mean age = 9.86)	94	134			1
				Reading Comprehension		0.79	0.395	0.79 (0.57–0.99)	0.00 (0.00–0.16)	0.26 (0.19–0.36)	7.4–12.3 (mean age = 9.86)	94	134			1
				Reading Comprehension		0.68	0.34	0.68 (0.30–0.77)	0.00 (0.00–0.21)	0.42 (0.32–0.56)	7.4–12.3 (mean age = 9.86)	94	134			1
47	Keenan et al., 2006	USA	CLDRC	General reading - Letter/Word knowledge	All	0.77	0.44	0.66 (0.42–0.82)	0.11 (0.00–0.32)	0.23 (0.17–0.33)	8–17 (mean age = 11)	70	121			1
				Reading Comprehension		0.69	0.435	0.51 (0.26–0.74)	0.18 (0.00–0.41)	0.31 (0.23–0.42)	8–17 (mean age = 11)	70	121			1
48	Little et al., 2016	USA	FTP-R	Reading Comprehension	All	0.67	0.45	0.52 (0.37–0.67)	0.14 (0.02–0.27)	0.34 (0.29–0.39)	From 3rd grade to 7th grade (mean age = 11.75)	865	1782			1

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Table 1 (*continued*)

Study_ID	AUTHOR	Country[1]	Cohort[2]	Reading-related neurocognitive skill	Sex[3]	rMZ	rDZ	A (h^2)	C (c^2)	E (e^2)	Age_correct	MZ_Sample_Pairs	DZ_Sample_Pairs	School Grade Level[4]	Sex[5]	Spoken Language[6]
				Reading Comprehension		0.75	0.49	0.55 (0.43−0.68)	0.20 (0.09−0.30)	0.25 (0.22−0.29)	From 3rd grade to 7th grade (mean age = 11.75)	865	1782			1
49	Petrill and Thompson, 1994	USA	WRTP	General reading	All	0.84	0.565	0.55	0.29	0.16	6 - 13 (mean age = 9.55)	148	135			1
				Spelling		0.84	0.53	0.62	0.22	0.16	6 - 13 (mean age = 9.55)	148	135			1
				General reading		0.87	0.64	0.46	0.41	0.13	6 - 13 (mean age = 9.55)	148	135			1
				Language		0.72	0.455	0.53	0.19	0.28	6 - 13 (mean age = 9.55)	148	135			1

MZ = monozygotic twin; DZ = dizygotic twin; A = additive genetic component; C = shared environment component; E = unique environment component.

[1] USA = United States of America; Scandinavia = Sweden and Norway; UK = United Kingdom.

[2] CLDRC = Colorado Learning Disabilities Research centre twin study; ILTS = International Longitudinal Twin Study; CFR = Colorado Front Range; FTP-R = Florida Twin Project on Reading; WRRP = Western Reserve Reading Project; WRRMP = Western Reserve Reading and Math Project; FSTR = Florida State Twin Registry; TEDS = Twins Early Development Study; USC = University of Southern California; ATR = Australian Twin Registry; NTR = Netherlands Twin Register; CTR = Colorado Twin Register; CTSRD = Chinese Twin Study of Reading development; FTPRBE = Florida Twin Project on Reading. Behavior. and Environment; VTSABD = Virginia Twin Study of Adolescent Behavioral Development; QNTS = Quebec Newborn Twin Study; FTP-BE = Florida Twin Project on Behavior and Environment.

[3] All = Males and Females; F = Females; M = Males; OS = Opposite sex.

[4] 1=preschool/kindergarten; 2=elementary school (Grades 1–5); 3=middle school (Grades 6–8); 4=high school (Grades 9–12).

[5] 1=female; 2=male.

[6] 1=English speaking sample; 2 = non-English speaking sample.

samples (n = 44); the other studies were based on non-English-speaking samples (n = 5), with two studies on Chinese-, two studies on Dutch-, and one study on French-speaking samples. The total sample size, only counting independent studies, was 15,990 MZ individuals and 22,680 DZ individuals, with a total sample size of 38,670. The samples covered a wide age range, from 4.1 years to 18.5 years.

3.2. *Meta-analytic estimates*

Table 2 provides an overall summary of meta-analytic estimates for both reading and reading-related neurocognitive components.

3.2.1. *General reading*

Forty-eight articles were included in the analysis (Table 1). General reading's meta-analysis yielded an overall MZ correlation of 0.79 ($ESZ_{MZ} = 1.08$, S.E. = 0.09, t = 11.92, $p < 0.001$, 95 % CI = 0.90–1.26) and an overall DZ correlation of 0.46 ($ESZ_{DZ} = 0.50$, S.E. = 0.02, t = 29.23, $p < 0.001$, 95 % CI = 0.47−0.54). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: overall heritability of 66 %, shared environment effect of 13 %, and non-shared environment effect (including measurement error) of 21 %. We next assessed whether the magnitude of MZ and DZ correlations is moderated by school grade levels, sex, and spoken language. School grade levels moderated the magnitude of both MZ and DZ correlations (Table 3); although the ratio of the observed correlations (Astrom et al., 2007) between elementary and middle schools suggest that the stability of general reading skills is due largely to heritable influences (MZ = 0.68/0.76 = 0.89 and DZ = 0.41/0.48 = 0.85), about 15 % of the variation in general reading performance during middle school is independent of general reading performance in elementary school. Meta-analytic MZ and DZ correlations of this moderator showed a decrease of both heritability and shared environmental effects, and an increase in non-shared environmental effects (encompassing measurement error), from elementary school to middle school (Table 3). On the contrary, neither sex nor or spoken language moderated the magnitude of MZ and DZ correlations (Table 3), indicating that genetic and environmental influences are similar for boys and girls, and spoken languages.

3.2.1.1. Letter-word knowledge. Thirty-two articles were included in the analysis (Table 1). Letter-word knowledge meta-analysis yielded an overall MZ correlation of 0.79 ($ESZ_{MZ} = 1.08$, S.E. = 0.06, t = 17.98, $p < 0.001$, 95 % CI = 0.96–1.20) and an overall DZ correlation of 0.48 ($ESZ_{DZ} = 0.53$, S.E. = 0.03, t = 17.73, $p < 0.001$, 95 % CI = 0.47−0.59). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: 62 % heritability, 17 % shared environmental effect, and 21 % of phenotypic variance accounted by non-shared environmental factor and measurement error. Sex did not moderate the magnitude of MZ and DZ correlations (Table 3), indicating no significant differences in genetic or environmental effects between boys and girls.

3.2.1.2. Phonological decoding. Thirteen articles were included in the analysis (Table 1). Phonological decoding meta-analysis yielded an overall MZ correlation of 0.78 ($ESZ_{MZ} = 1.04$, S.E. = 0.07, t = 13.99, $p < 0.001$, 95 % CI = 0.88–1.19) and an overall DZ correlation of 0.44 ($ESZ_{DZ} = 0.47$, S.E. = 0.03, t = 16.51, $p < 0.001$, 95 % CI = 0.41−0.52). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: an overall heritability of 68 %, shared environment effects of 10 %, and non-shared environment effects (including measurement error) of 22 %.

3.2.1.3. Reading comprehension. Thirty-two articles were included in the analysis (Table 1). Reading comprehension meta-analysis yielded an overall MZ correlation of 0.79 ($ESZ_{MZ} = 1.07$, S.E. = 0.15, t = 6.96, $p <$

Table 2
Meta-analytic estimates for the different neurocognitive components.

Cognitive ability	Number of studies	Heritability	Shared environment	Non-shared environment
General Reading	48	66 %	13 %	21 %
Letter-Word Knowledge	32	62 %	17 %	21 %
Phonological Decoding	13	68 %	10 %	22 %
Reading Comprehension	32	68 %	11 %	21 %
PA	13	52 %	23 %	25 %
RAN	11	46 %	15 %	39 %
Spelling	15	80 %	0%	20 %
Language	10	34 %	47 %	19 %

PA = phonological awareness; RAN = rapid automatized naming.

0.001, 95 % CI = 0.77–1.38) and an overall DZ correlation of 0.45 (ESZ_{DZ} = 0.49, S.E. = 0.03, t = 19.89, p < 0.001, 95 % CI = 0.44–0.54). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: an overall heritability of 68 %, 11 % of variance explained by shared environment effects, and 21 % by non-shared environment effects and measurement error. Moderators analysis showed that school grade levels moderated the magnitude of both MZ and DZ correlations (Table 3); although the ratio of the observed correlations (Astrom et al., 2007) between elementary and middle schools suggest that the stability of general comprehension skills is due largely to heritable influences (MZ = 0.62/0.76 = 0.82 and DZ = 0.39/0.50 = 0.78), about 20 % of the variation in reading comprehension performance during middle school is independent of reading comprehension performance in elementary school. Meta-analytic MZ and DZ correlations of this moderator showed a decrease of both heritability and shared environmental effects, and an increase in non-shared environmental effects (encompassing measurement error), from elementary school to middle school (Table 3).

3.2.2. PA

Thirteen articles were included in the analysis (Table 1). PA meta-analysis yielded an overall MZ correlation of 0.75 (ESZ_{MZ} = 0.97, S.E. = 0.12, t = 8.04, p < 0.001, 95 % CI = 0.73–1.22) and an overall DZ correlation of 0.49 (ESZ_{DZ} = 0.54, S.E. = 0.03, t = 16.28, p < 0.001, 95 % CI = 0.47–0.60). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: an overall heritability of 52 %, an overall shared environmental effect of 23 %, and an overall non-shared environmental effect of 25 % (including measurement error). Moderators analysis showed that school grade levels moderated the magnitude of both MZ and DZ correlations (Table 3); although the ratio of the observed correlations (Astrom et al., 2007) between preschool/kindergarten and elementary school suggest that the stability of PA skills is due largely to heritable influences (MZ = 0.62/0.86 = 0.72 and DZ = 0.41/0.60 = 0.68), about 30 % of the variation in PA performance during elementary school is independent of PA performance in preschool/kindergarten. Meta-analytic MZ and DZ correlations of this moderator showed a decrease of both heritability and shared environmental effects, and an increase in non-shared environmental effects (encompassing measurement error), from preschool/kindergarten to elementary school (Table 3).

3.2.3. RAN

Eleven articles were included in the analysis (Table 1). RAN meta-analysis yielded an overall MZ correlation of 0.61 (ESZ_{MZ} = 0.71, S.E. = 0.06, t = 12.53, p < 0.001, 95 % CI = 0.59–0.83) and an overall DZ correlation of 0.38 (ESZ_{DZ} = 0.40, S.E. = 0.08, t = 4.90, p < 0.001, 95 % CI = 0.23–0.57). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: an overall heritability of 46 %, an overall effect of 15 % for shared environment and of 39 % for non-shared environment (including measurement error).

3.2.4. Spelling

Fifteen articles were included in the analysis (Table 1). Spelling abilities meta-analysis yielded an overall MZ correlation of 0.79 (ESZ_{MZ} = 1.08, S.E. = 0.20, t = 5.56, p < 0.001, 95 % CI = 0.69–1.48) and an overall DZ correlation of 0.39 (ESZ_{DZ} = 0.42, S.E. = 0.03, t = 13.00, p < 0.001, 95 % CI = 0.35–0.48). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: an overall heritability of 80 %, an overall effect of 0% for shared environment and of 20 % for non-shared environment (including measurement error).

3.2.5. Language

Ten articles were included in the analysis (Table 1). Language skills meta-analysis yielded an overall MZ correlation of 0.81 (ESZ_{MZ} = 1.13, S.E. = 0.14, t = 7.81, p < 0.001, 95 % CI = 0.83–1.42) and an overall DZ correlation of 0.64 (ESZ_{DZ} = 0.75, S.E. = 0.09, t = 8.59, p < 0.001, 95 % CI = 0.57–0.93). The Falconer's formula (Falconer, 1960) applied to meta-analytic MZ and DZ correlations produced: an overall heritability of 34 %, an overall effect of 47 % for shared environment and of 19 % for non-shared environment and measurement error.

4. Discussion

In this comprehensive meta-analysis, we synthesized the results of behavioral genetic research on reading-related skills of 49 twin studies spanning 4.1–18.5 years of age, with a total sample size of more than 38,000 individuals. Our results indicate a similar pattern of causal architecture across most of the reading-related neurocognitive functions analyzed by these studies, with moderate-to-substantial meta-heritability estimates, smaller environmental contributions, a significant effect of school grade levels, and no significant effects of moderators such as sex, and spoken language. This could in part be due to the fact that the genetic covariance among these neurocognitive components is high (Byrne et al., 2007, 2009; Gayan and Olson, 2003; Harlaar et al., 2010; Betjemann et al., 2008; Davis et al., 2001; Plomin and Kovas, 2005).

Specifically, the phenotypic variance of general reading, letter-word knowledge, phonological decoding, reading comprehension, PA, RAN, and spelling, was primarily explained by additive genetic and non-shared environmental factors, while shared environment appeared to play a less important role. These findings support the notion that the phenotypic variance of several reading-related neurocognitive components could be captured by the following equation: $a^2 > e^2 > c^2$ (Plomin and Daniels, 2011). These meta-analytic results agree with the well-established notion that the contribution of shared environmental influences is in general relatively small, and accounts for lower phenotypic variance compared to the non-shared environmental influences in reading skills (Bishop, 2015; Olson, 2002; Olson et al., 2013; Willcutt et al., 2010). Nonetheless, the classical twin approach is known to have only limited power to detect shared environmental effects (Martin et al., 1978; Visscher et al., 2008). The results of the meta-analysis of the twin correlations result in a heritability above 50 % for general reading, letter-word knowledge, phonological decoding, reading comprehension, PA, RAN, and spelling, suggesting that there is indeed a robust genetic effect on these reading-related skills (Plomin and Daniels, 2011). Furthermore, our findings support the notion that more research is now needed to specifically distill what unique environmental effects create

Table 3
Results for the univariate moderator analyses.

Neurocognitive component	Moderator	Category	Number of Studies	MZ						DZ						Meta-analytic estimates		
				$F_{(df)}$	*p-value*	ESz	95 % CI		rMZ	F(df)	*p-value*	ESz	95 % CI		rDZ	Heritability	Shared environment	Non-shared environment
	School grade level	Elementary	25	$5.49_{(1,120)}$	0.02	1.00	0.91	1.10	0.76	$9.89_{(1,128)}$	0.002	0.52	0.48	0.57	0.48	0.56	0.20	0.24
		Middle	8			0.83	0.68	0.98	0.68			0.43	0.40	0.51	0.41	0.54	0.14	0.32
General Reading	Sex	Girls	8	$0.01_{(1,28)}$	0.91	0.99	0.87	1.11	0.76	$1.62_{(1,28)}$	0.21	0.55	0.48	0.63	0.50	–	–	–
		Boys				1.00	0.88	1.12	0.76			0.52	0.44	0.59	0.48	–	–	–
	Spoken Language	English	44	$0.10_{(1,181)}$	0.75	1.01	0.82	1.20	0.77	$0.70_{(1,194)}$	0.40	0.49	0.44	0.53	0.45	–	–	–
		Non-English	5			1.07	0.87	1.27	0.79			0.51	0.47	0.54	0.47	–	–	–
Letter-Word Knowledge	Sex	Girls	6	$0.32_{(1,12)}$	0.58	0.96	0.72	1.20	0.74	$0.39_{(1,12)}$	0.55	0.56	0.44	0.69	0.51	–	–	–
		Boys				0.98	0.74	1.22	0.75			0.53	0.41	0.66	0.49	–	–	–
Reading Comprehension	School grade level	Elementary	15	$18.38_{(1,46)}$	<0.001	1.00	0.92	1.10	0.76	$19.43_{(1,49)}$	<0.001	0.55	0.46	0.64	0.50	0.52	0.24	0.24
		Middle	7			0.72	0.58	0.85	0.62			0.41	0.31	0.51	0.39	0.46	0.16	0.38
PA	School grade level	Preschool/Kindergarten	5	$8.91_{(1,21)}$	0.01	1.29	0.81	1.77	0.86	$10.27_{(1,22)}$	0.004	0.69	0.53	0.85	0.60	0.52	0.34	0.14
		Elementary	5			0.73	0.28	1.18	0.62			0.44	0.29	0.59	0.41	0.42	0.20	0.38

ESz = Fisher's Z score; MZ = monozygotic twins; DZ = dizygotic twins; CI = confidence interval; h^2=heritability; c^2= shared-environment; e^2= non shared environment PA = Phonological Awareness.

individual differences in children growing up in the same family (Burt, 2009; Plomin and Daniels, 2011; Scaini et al., 2012). As genetic and environmental influences are not mutually exclusive, future research will be important to ascertain multiple aspects of gene-environment interplay, perhaps most importantly gene-environment correlation (rGE) and gene-environment interaction (GxE) in reading-related skills. Recent twin studies highlight the importance of environmental influences in understanding children's school performance and suggest parental education, home chaos and neighbourhood conditions as a potential moderators of reading achievement (Friend et al., 2008; Taylor and Hart, 2014; Little et al., 2019). Interestingly, some investigations provided evidence of interactions between candidate genetic regions/markers and some environmental measures (i.e. home language/literacy environment, maternal smoke during pregnancy, birth weight and socio-economic status) on reading- and language-related phenotypes (McGrath et al., 2007; Mascheretti et al., 2013, 2018).

A relatively different pattern applied to language skills, for which the phenotypic variance could be primarily explained by shared environmental factors and additive genetic effects. These findings agree with previous data showing that early childhood language as well as the continuity between early and middle childhood language, are strongly influenced by shared environment, while additive genetic factors account for just one-third of the variance (Hayiou-Thomas, 2008, 2012; Byrne et al., 2009; Olson et al., 2011; Hart et al., 2009a,b).

Moderator analyses revealed that the MZ and DZ twin correlations upon general reading, reading comprehension, and PA, differed among school grade levels. Our results show a decrease of genetic and shared environmental influences and an increase of non-shared environmental effects from preschool/kindergarten through elementary school to middle school, suggesting greater importance of family effects in preschool and in early school years. However, after the initiation of formal schooling, heritability estimates slightly decrease -although remaining substantial- and shared environmental effects decline, leaving the non-shared environment as the primary sources of variability in reading (Harlaar et al., 2007;Haworth et al., 2009;Hart et al., 2013a,b;Olson et al., 2014). Although the ratio between MZ and DZ correlations for each significant moderator suggested substantial genetic stability, about 20–30 % of the variation in reading-related neurocognitive skills was plausibly due to additional influences. These findings were highly consistent with previous works showing that, though about two thirds of the stability of reading-related neurocognitive components in reading (dis)ability was due to genetic influences, age-specific as well as school grade-specific genetic influences showed significant effects (Wadsworth et al., 2001, 2007; Harlaar et al., 2007; Astrom et al., 2007; Byrne et al., 2007, 2009; Hayiou-Thomas et al., 2010; Soden et al., 2015; Christopher et al., 2016; Erbeli et al., 2018; Tosto et al., 2017). One possible explanation of this significant change in twin correlations could be that these "new'' genetic influences are concomitant with changes in cognitive and reading development as well as with environmental (e.g. school) demands (Harlaar et al., 2007; Astrom et al., 2007; Byrne et al., 2007, 2009; Hayiou-Thomas et al., 2010; Soden et al., 2015; Christopher et al., 2016; Erbeli et al., 2018; Tosto et al., 2017). Reading and reading-related neurocognitive components are dynamic processes developing through several stages from preschool to high school. Under Chall's widely accepted theory of the stages of reading development (Chall, 1983), after the prereading stage (from birth to elementary school), children pass through two major developmental phases: "learning to read" (early years of the elementary school) followed by "reading to learn" (later years of the elementary school/middle school). During the "learning to read" phase, children develop knowledge of print structure, basic understanding of the rules of language, word decoding skills, and practice fluent reading skills. The transition from the "learning to read" phase to the "reading to learn" phase comprises the mastery of fluent reading skills along with the integration of new knowledge and information from what is being read (Chall, 1983; Biancarosa and Snow, 2004; Betjemann et al., 2008). During the final stages (high school), reading strategies increasingly contribute to the successful integration of new ideas, to understanding complex concepts, and to making judgments about content that is read (Chall, 1983). Thus, it is plausible that "new'' genetic influences and/or changes in cognitive development as well as in environmental (e.g. school) demands, may affect the transition through reading development. Regarding PA, it is possible that "new" genetic influences, such as those associated with specific reading skills that develop incrementally during first grade, may turn on, or that general processing skills needed for decoding (e.g. related to increased working memory demands) emerge anew in elementary school (Erbeli et al., 2018). Concerning reading comprehension, "new" genetic effects may come online, or "new" and more complex cognitive skills (such as inference, comprehension monitoring, and knowledge and use of story structure) emerge anew in middle school reading (Oakhill and Cain, 2012; Erbeli et al., 2018).

Finally, no significant differences have been reported between English and non-English-speaking samples suggesting lack of significant language differences in accounting for the heritability of general reading skills (Wong et al., 2014; Chow et al., 2011). Similarly, no significant differences emerged for sex as a moderator for the general reading and letter-word knowledge components. These meta-analytic findings support previous studies providing no evidence for a differential etiology of reading skills as a function of sex (Hawke et al., 2007. Hawke et al., 2006; Wadsworth et al., 2000).

Several limitations should be noted. First, we conducted our literature research only in Medline and PsychInfo databases; this could have limited the number of retrieved records. Second, meta-analyses are inevitably constrained by the nature of the studies upon which they are based. Although meta-analyses are meant to provide objective appraisals of the state of the art in a specific field, there are many steps that involve highly subjective choices. These include the collection of the studies, the criteria for eligibility, the choice of assessment criteria, and the outcome measures. All these aspects could affect the objectivity of the results (Verweij et al., 2010). Third, because of the limited number of published studies, we could not test for the moderators' effect in all the reading-related neurocognitive components. Since most of the included studies were conducted in English-speaking samples, special cautiousness should be taken in generalizing these findings to non-English-speaking populations. Further work needs to be done to establish heritability estimates in non-English-speaking populations. Fourth, not all studies included in this meta-analysis reported twin correlations of the full ACE model, which may have inflated the overall heritability estimates (Posthuma and Boomsma, 2000). However, only five studies (Bates et al., 2004; Harlaar et al., 2005; van Leeuwen et al., 2009; Malanchini et al., 2017; Taylor and Schatschneider, 2010) reported their correlations based on best-fitting (reduced) models, which should limit their impact on the general meta-heritabilities. Fifth, only published papers were analyzed, whereas data from the unpublished studies were not included. Although this choice allowed controlling for study quality, it could exclude gray literature that could also be informative for our analyses.

5. Conclusions

Taken together, our meta-analytic approach shows that genetic as well as non-shared environmental factors contribute to individual differences in reading-related neurocognitive components. Except for language for which shared environment seems to play a more important role, the causal architecture across most of the reading-related neurocognitive components can be represented by the following equation $a^2 > e^2 > c^2$. Moderators analysis revealed that sex and spoken language did not affect the heritability of any reading-related skills; on the contrary, school grade levels moderated the heritability of general reading, reading comprehension, and PA skills.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgements

CA was supported by the Italian Ministry of Health Grant RC2019. SM was supported by the Italian Ministry of Health Grant RC2019 and RC2020.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neubiorev.2020.11.016.

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