Published in final edited form as:
Intelligence. 2017 November ; 65: 67–74. doi:10.1016/j.intell.2017.08.005.

Approximate Number Sense Shares Etiological Overlap with Mathematics and General Cognitive Ability

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Abstract

Approximate number sense (ANS), the ability to rapidly and accurately compare quantities presented non-symbolically, has been proposed as a precursor to mathematics skills. Earlier work reported low heritability of approximate number sense, which was interpreted as evidence that approximate number sense acts as a fitness trait. However, viewing ANS as a fitness trait is discordant with findings suggesting that individual differences in approximate number sense acuity correlate with mathematical performance, a trait with moderate genetic effects. Importantly, the shared etiology of approximate number sense, mathematics, and general cognitive ability has remained unexamined. Thus, the etiology of approximate number sense and its overlap with math and general cognitive ability was assessed in the current study with two independent twin samples (N = 451 pairs). Results suggested that ANS acuity had moderate but significant additive genetic influences. ANS also had overlap with generalist genetic mechanisms accounting for variance and covariance in mathematics and general cognitive ability. Furthermore, ANS may have genetic factors unique to covariance with mathematics beyond overlap with general cognitive ability. Evidence across both samples was consistent with the proposal that the etiology of approximate number sense functions similar to that of mathematics and general cognitive skills.

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Introduction

Approximate number sense (ANS) refers to the ability to rapidly and accurately compare quantities presented non-symbolically. The acuity of the comparison of approximate quantities follows Weber's law. That is, discrimination between two stimuli increases linearly with stimulus intensity, as do other psychophysical comparisons. Weber's law has been shown to apply to quantity discriminations at both a behavioral and neural level (Dehaene, 2003). Therefore, scores from non-symbolic comparison tasks are often interpreted as a Weber fraction, which represents the just-noticeable difference between two quantities for a given individual. Behavior consistent with this property of ANS has been found in several non-human animals, including dolphins and chimpanzees (e. g. Boysen & Hallberg, 2000; Kilian, Yaman, von Fersen, & Güntürkün, 2003). Given its presence in animals and humans, numerous authors have hypothesized about the evolutionary importance of approximate number sense, for example deciding which of two trees has a greater amount of food (Halberda, Mazzocco, & Feigenson, 2008). Interest in ANS also stems from initial evidence that ANS may be an important precursor of later symbolic math skills (Halberda, Mazzocco, & Feigenson, 2008). Despite its purported evolutionary importance and possible link to formal mathematics, only one study to date has examined the influence of genetic and environmental factors on individual differences in ANS (Tosto et al., 2014). Here we use the twin methodology to estimate the effects of genetic, shared environmental, and nonshared environmental influences to replicate previous research on individual variation in ANS in two new samples. Next, we extend this approach to examine covariance of ANS with mathematics and whether covariance with mathematics relates to general cognitive ability.

Research examining the development of mathematics has long sought to identify a single, early developing, domain-specific cognitive skill that strongly predicts later math outcomes in formal schooling. ANS has several of these characteristics. ANS is present prior to formal mathematics education (Barth, La Mont, Lipton, Dehaene, Kanwisher, & Spelke, 2006; Gilmore, McCarthy, & Spelke, 2007), and important to the current study, there are measurable individual differences in ANS acuity (e.g. Halberda & Feigenson, 2008; Halberda, Ly, Wilmer, Naiman, & Germine, 2012; Price, Palmer, Battista, & Ansari, 2012). Moreover, several studies have found a unique effect of ANS acuity in predicting math achievement both concurrently and retrospectively (e. g. Halberda, Mazzocco, & Feigenson, 2008) and prospectively (Mazzocco, Feigenson, & Halberda, 2011a), supporting the domain-specific hypothesis. However, results have been mixed; with others finding no such unique effects of ANS in predicting math achievement (see De Smedt, Noel, Gilmore, & Ansari, 2013 for review of positive and negative results and Schneider et al. (2017) for a recent meta-analysis). Many of the studies that do not find unique effects of ANS have instead implicated other symbolic mathematical skills or general cognitive mechanisms as accounting for variance in math achievement. For example,Gilmore et al. (2013) argued that ANS trials where quantity and surface area are incongruent drive the relationship between ANS and math performance, suggesting inhibitory control, not ANS acuity, predicts math achievement, and supporting a more domain-general view of ANS. The question of whether

ANS represents a domain-general or domain-specific predictor of mathematics remains an open debate.

The etiology of ANS is understudied. Tosto et al. (2014) reported modest but significant genetic contributions to individual differences in ANS acuity using traditional twin analyses. Follow up analyses using genome-wide complex-trait analysis, a newer molecular approach that does not rely on twins, failed to recover significant genetic effects for ANS acuity. This led the authors to hypothesize that ANS was an evolved, fitness trait. Classical quantitative genetic theory posits fitness traits have low heritability due to their importance for survival and can be conserved across species (Fisher, 1930; Falconer, 1960). In a fitness trait, heritability has been constrained by evolutionary processes (see Merila & Sheldon (1999) for a review of empirical findings relative to fitness and heritability). Further evidence of conservation across species was noted by Jones et al. (2014) which found similar levels of ANS acuity between species of lemurs and Old World monkeys. However, while Jones and colleagues (2014) found that mean ANS performance was similar across species, there was also notable individual differences within each species. Tosto et al. (2014) reconciled the contention that ANS is a fitness trait (with low or non-significant heritability shaped by evolution) with the considerable variation within the population by proposing that unique environmental influences drive individual differences. This view leads to a specific, testable, hypothesis about the etiological link between ANS and other cognitive traits. Namely, ANS acuity would not be expected to have genetic overlap with general cognitive predictors of math, because these traits are known to have moderate heritability, and only about a quarter of the variance in general cognitive ability is attributable to non-shared environmental factors (Bouchard & McGue, 1981; Plomin, 1999). Rather, this view predicts that the majority of the overlap of ANS with mathematics and general cognitive ability would be expected to come from environmental factors. Previous work did not consider the etiological overlap of ANS with mathematics achievement or the extent to which ANS also has genetic overlap with general cognitive ability. Thus, the current study examined this overlap, in an effort to better characterize the shared etiology of ANS, mathematics, and general cognitive ability.

In comparison to the single published study on the genetic and environmental etiology of ANS, the last decade has seen a proliferation of research examining the etiological underpinnings of mathematics achievement. Results have suggested that mathematics has moderate genetic influences (Hart et al., 2009; Haworth et al., 2007; Haworth et al., 2009; Knopik & DeFries, 1999; Thompson, Detterman, & Plomin, 1991; Wadsworth, DeFries, Fulker, & Plomin, 1995). There is also some evidence of significant shared environmental influences (factors that make twins within the same family similar, but different between families; Hart et al., 2009; Petrill et al., 2012). The remainder of the variance is accounted for by nonshared environmental influences (factors that make twins within the same family different). Twin studies have also been employed to examine the etiological overlap of mathematics and general cognitive ability. A particularly influential proposal, the generalist genes hypothesis (Plomin & Kovas, 2005), suggests a shared set of genetic factors account for large portions of the overlap across multiple cognitive traits. For example,Hart et al. (2009) found evidence for generalist genes by examining the considerable genetic overlap between general cognitive ability, reading, and mathematics. Furthermore,Haworth et al.

(2009) found that the same generalist genetic factors were responsible for overlap in the low ability range of math skills, as were operating throughout the entire distribution. Together, previous behavioral genetic analyses suggest that across the range of individual differences, mathematics has moderate genetic influences and exhibits similar patterns of inheritance as general cognitive ability.

The present study sought to examine the shared etiology of ANS acuity, math achievement, and general cognitive ability in two twin samples. The first aim of these analyses was to replicate the univariate findings of Tosto et al. (2014). ANS acuity was expected to have modest but significant genetic influences, non-significant shared environmental variance, and significant nonshared environmental influences (which include error), similar to those previously reported in Tosto et al. (2014). The second aim of the study was to examine etiological overlap of ANS acuity and mathematics achievement in both samples. Math story problem solving and math fluency were the math outcomes of interest in the current study because they were assessed in both samples and represent two important domains of formal mathematics instruction. Examining overlap across two math domains allowed for testing the robustness of the etiological relationships. We expected to find mostly environmental overlap between ANS and math achievement because if ANS acts a fitness trait then much of the overlap with math would be expected to be attributable to nonshared environmental influences. Importantly, the third aim of the study was to examine if the etiology of general cognitive ability overlaps with ANS acuity and mathematics. If ANS is a fitness trait, having no or low heritability that contributes to individual differences, as proposed by Tosto et al (2014) then variation in ANS would not be expected to be related to genetic factors. Therefore, we would not expect ANS to have significant shared genetic influences with general cognitive ability, a classic trait with moderate genetic influences (Bouchard & McGue, 1981; Plomin, 1999). Rather, similar to the prediction for the overlap of mathematics and ANS, here we would also expect the overlap to stem mostly from overlap in nonshared environmental factors. Thus, over the course of a systematic set of analyses in two separate samples the present study aims to expand understanding of the etiological links between ANS, math achievement, and general cognitive ability.

Methods – Western Reserve Reading and Math Project

Participants

Participants included N = 105 monozygotic (MZ) twin pairs and N = 143 same-sex dizygotic (DZ) twin pairs from the Western Reserve Reading and Math Project (WRRMP; Petrill, Deater-Deckard, Thompson, DeThorne, & Schatschneider, 2006). Twins were tested in their homes by trained research assistants in separate rooms. Participants were a mean age of 12.25 years (SD = 1.20, Range = 8.75 to 15.33). The sample was 59.7% female. Consistent with our prior publications involving mathematics data (Hart et al., 2009; Petrill et al., 2012), we residualized raw scores for sex, age, age squared, school months and school months squared using a regression procedure.

Measures

Approximate number sense—Approximate number sense was measured with the Panamath task (Halberda, Mazzocco, & Feigenson, 2008). The task involved sets of yellow and blue dots interspersed and the participant indicated via button press whether there were more yellow or blue dots. Participants had 300ms to respond in each trial. The color of the more numerous dot varied randomly and half the trials were area-controlled, while the remaining trials were size controlled, matching the procedure of Halberda et al. 2008. Participants completed 110 trials across two blocks, one administered at the start of the visit and the other administered at the end of the visit (approximately three hours apart), as recommended by task developers (J. Halberda, *personal communication*, 2008). Weber fractions were calculated using a built in macro which took into account all trials across the blocks, using methods detailed in Halberda et al., 2008. To better approximate a normal distribution scores were log transformed in subsequent analyses. Moreover, because a larger Weber fraction represents poorer acuity, raw scores were reversed (multiplied by -1) so that higher scores would represent higher skill in both ANS acuity and math performance.

Mathematics achievement—Two measures of math achievement from the Woodcock Johnson III Tests of Achievement (Woodcock, McGrew, & Mather, 2001) were utilized. The Applied Problems subtest assessed ability to solve math story problems. Children were presented a series of math story problems visually and read aloud that required the children to solve questions of increasing difficulty. Problems included counting, geometric shape identification, and single and multistep word problems requiring a variety of mathematical operations and concepts. The task includes solving problems with whole numbers, fractions, and decimals. There was no time limit for completion for items or the task overall. The published median reliability of this task is 0.92 in the 5- to 19-year-old age range. The Math Fluency subtest assessed ability to solve single-digit addition, subtraction, and multiplication items in a timed setting with pencil and paper. Participants had 3 minutes to complete as many problems as they could out of a set of 160 items. The published median reliability for this test is 0.89 for the 7- to 19-year-old age range.

General cognitive ability—An IQ test was not included in the same assessment point as the measurement of approximate number sense and mathematics achievement. However, *g* can be ascertained from the same time point by utilizing the first principal component of several non-math and non-number sense measures that were assessed concurrently, consistent with Spearman's conceptualization of general cognitive ability. Measures from the current wave of data collection and an earlier measurement occasion that focused on reading achievement and was typically administered within four weeks prior (M = 17.94 days, SD = 16.49), were used to construct a factor score that was representative of *g*. Five measures were used: the Boston Naming Test (Kaplan, Goodglass, & Weintraub, 1983), Clinical Evaluation of Language Fundamentals (CELF) Word Classes subtest (Semel, Wiig, & Second, 2003), Woodcock Reading Mastery Test – Revised (WRMT-R) Word Identification subtest (Woodcock, 1998), Wechsler Intelligence Scale for Children (WISC) Symbol Search subtest (Wechsler et al., 2004), and Comprehensive Test of Phonological Processing (CTOPP) Rapid Digit Naming and Rapid Letter Naming subtests (Wagner, Torgesen, & Rashotte, 1999). The Boston Naming Test, CELF Word Classes, and WRMT-R

Word Identification tasks were administered in the visit prior to the ANS and mathematics assessments, whereas WISC Symbol Search, and CTOPP Rapid Digit Naming and Rapid Letter Naming were administered in the same session as the ANS and mathematics measures. *g* accounted for 49.4% of the variance among the measures. This approach has been used previously (Lukowski et al., 2014) to examine overlapping and unique effects of working memory components and mathematics above and beyond general cognitive ability.

Results – Western Reserve Reading and Math Project

Descriptive statistics of the measures are displayed in the upper panel of Table 1. Standard scores for the math measures suggest that the distribution of scores in the sample was similar to what would be expected in the population. After transformation there is still some evidence of relatively larger skew and kurtosis in the ANS values, but in general the assumption of normality can be retained. Consistent with previous research, we found significant phenotypic correlations between approximate number sense and math achievement (see Table 2, upper panel). Intraclass correlations (see Table 2) were also calculated (rMZ shows the correlation of monozygotic twin pairs and rDZ shows the correlation of dizygotic twin pairs). Briefly, the twin design allows for the estimation of genetic and environmental variance by examining the covariance between sets of monozygotic and dizygotic twins. Monozygotic twins share 100% of their segregating genes (A, additive genetics), 100% of their shared environments (C, environmental influences which make twins similar within a family but different between families), and 0% of their nonshared environment (E, influences that are unique for each child within families). In comparison, dizygotic twins share on average 50% of their additive segregating genes, but like monozygotic twins have 100% their shared environments in common and 0% of their nonshared environments in common.

Intraclass correlations showed the expected pattern; MZ twins were more similar than DZ twins, suggesting genetic influences on all traits. Also of note, the MZ correlation for ANS was much lower than that of mathematics and general cognitive ability, which suggested that larger estimates of nonshared environments might be expected for ANS, though all traits were predicted to have nonshared environmental effects (which include measurement error).

These genetic and environmental components of variance and covariance were examined more formally utilizing structural equation modeling techniques in Mx (Neale, Boker, Xie, & Maes, 2006). Structural equation models allow these latent genetic (A), shared environmental (C) and nonshared environmental factors (E) to be estimated. For each measure an ACE model was fit to the data and in order to avoid overfitting the data we also examined an AE model[1], as an AE model was suggested by Tosto et al. (2014) for individual differences in ANS acuity. ACE and AE models were compared using a chi-square test of the negative log likelihood of the models; an AE model was retained when excluding C did not result in a significant decrease in fit. Estimates for the best fitting models are shown in Table 3, upper panel. Similar to Tosto et al. (2014), the reduced AE

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[1] CE models were also fit, however, CE models showed no improvement in AIC over AE and ACE models, thus AE models were retained for ANS acuity

model was found to be the best fitting model for approximate number sense. Number sense had significant additive genetic influences and significant nonshared environmental influences. In comparison, an ACE model was best fitting for math achievement measures. Both math achievement measures had significant genetic and nonshared environmental influences, but differing from number sense there was also evidence of significant shared environmental influences. These findings were consistent with previous studies investigating ANS acuity (Tosto et al., 2014) and math achievement (e. g. Hart et al., 2009).

Beyond univariate results, a primary goal of the present study was to examine the bivariate relations between number sense and mathematical achievement. The bivariate ACE model allows the covariance between ANS acuity and math achievement to be broken into additive genetic (A), shared environmental (C), and nonshared environmental (E) latent factors. Because an AE model best fit number sense, shared environmental overlap (overlap in C) was not modeled. Results of the bivariate analysis are shown in Table 4, upper panel. The table shows standardized path estimates (values are unsquared as compared to the squared variance components reported in Table 3). a_1 represents latent genetic influences that account for variance in ANS acuity and its covariance with mathematics. a_2 represents latent genetic influences unique to mathematics. Similarly, e_1 represents latent nonshared environmental influences that account for variance in ANS acuity and covariance with mathematics. e_2 represents nonshared environmental influences unique to mathematics.

Of key interest was the extent to which latent genetic (A) and nonshared environmental (E) factors associated with ANS acuity also accounted for individual differences in math. This was examined by the overlap in a_1 and e_1, respectively. Results (see Table 4, upper panel) showed that number sense and math outcomes had significant genetic overlap ($a_1 = 0.58$ for ANS and math story problems, $a_1 = 0.35$ for ANS acuity and math fluency). In addition, while nonshared environmental factors were significant for each measure, there was no evidence for overlap between the measures ($e_1 = 0.02$ for ANS acuity and each math outcome).

Bivariate analyses indicated that there were genetic influences shared by number sense and math achievement. However, the question remained as to whether these influences represented generalist genes or whether latent genetic influences accounting for variance in number sense accounted for genetic influences on math separate from latent generalist genetic influences. Figure 1 depicts the full trivariate model to test these questions and estimates in Table 5 reflect the unsquared standardized path coefficients, which can be mapped directly onto this figure. Though order is somewhat arbitrary given that data were collected at the same time point, general cognitive ability was put in the first position to test for generalist genetic overlap. a_1 represents an additive genetic factor that accounts for variance in all three outcomes. Results in the first column of Table 5 show the path loading for each of the paths from this general genetic factor (a_1) to each construct. a_2 represents residual genetic variance in ANS and covariance between ANS and mathematics after accounting for shared variance with general cognitive ability. Results in the second column of Table 5 show the path loadings for each of the paths from this latent genetic factor (a_2) to ANS and mathematics. a_3 represents additive genetic factors unique to mathematics. Results in the third column of Table 5 show the path estimate for the residual genetic variance in mathematics (a_3) that does not covary with general cognitive of ANS factors. C and E have similar interpretations, for shared environmental factors and nonshared environmental factors. Full results are displayed in Table 5, upper panel. Of interest for the generalist genes proposal was the overlap found in a_1. These analyses provided evidence for generalist genes, as there was significant genetic overlap between *g*, number sense, and math story problems. Moreover, the trivariate analyses allowed for an examination of residual genetic overlap between ANS acuity and math after accounting for shared variance with general cognitive ability. Number sense did not have significant genetic influences on either math story problems ($a_2 = 0.25$) or math fluency ($a_2 = 0.27$) once accounting for genetic effects in common with general cognitive ability. Mathematics and general cognitive ability also had shared environmental overlap, found in c_1. Like in the bivariate analyses, nonshared environmental factors were largely unique to each construct.

Next we replicated these analytical methods in a second twin sample.

Methods – Colorado Learning Disabilities Research Center

Participants

N = 59 MZ and N = 144 DZ twin pairs from the Colorado Learning Disabilities Research Center (CLDRC) sample completed the approximate number sense assessment. CLDRC is an ongoing population-based study of the etiology of learning disorders (see Olson, 2006 for more details about the sample). In brief, permission was sought from parents of all twin pairs between 8 – 18 years in 22 local school districts to review school records. If either member of a twin pair had a history of reading or attention difficulties, the pair and any siblings were invited to participate in the study. A comparison group of control twins was selected from the overall sample of pairs who did not meet the screening criteria for learning problems. While the sample was recruited in part for being at risk for reading disability, the math scores of this subsample of participants do not differ meaningfully from the population mean in their math skills. Participants completed testing with separate research assistants during a visit to the lab with the research team. Mathematics and general cognitive ability were assessed in a lab visit timed typically 1 to 3 months prior to the approximate number sense assessment which was included in a second cognitive battery. Mean age of the sample was 11.13 years (SD = 2.39, Range = 8.18 – 16.88). The sample is 46.5% female. Like in WRRMP data, we residualized raw scores for sex, age, age squared, school months and school months squared using a regression procedure.

Measures

Approximate number sense—The Panamath task, containing yellow and blue dots interspersed, was also administered in the CLDRC sample. Participants completed one block of the task with between 96 to 120 trials depending on their age. Parameters for administration were also similar to Halberda et al. (2008).

Mathematics achievement—The same mathematics measures, the Woodcock-Johnson Tests of Achievement Applied Problems and Math Fluency subtests, were administered in the CLDRC sample.

General cognitive ability—General cognitive ability was assessed with the Wechsler Intelligence Scale for Children (Wechsler, 1991). The full scale IQ score from this scale was utilized in subsequent analyses.

Results – Colorado Learning Disabilities Research Center

While differences in the measures did not allow the samples to be directly combined, the same analytic approach was taken in the second sample. Descriptives are reported in Table 1, lower panel. Phenotypic and intraclass correlations in Table 2, lower panel, show a similar pattern of significant but modest correlations between number sense and math achievement measures, as was found in WRRMP.

Univariate analyses (see Table 3, lower panel) of number sense and math achievement also show a similar pattern to WRRMP. However, an AE model was found to be the best fitting model for all measures. Number sense, math story problem solving, and math fluency all had significant genetic and nonshared environmental influences.

Consistent with WRRMP, bivariate analyses (see Table 4, lower panel) indicated significant genetic overlap between number sense and math story problems ($a_1 = 0.34$) and math fluency ($a_1 = 0.26$). Likewise, there was no evidence for significant overlap of nonshared environmental influences ($e_1 = 0.00$ for both math outcomes).

The role of general cognitive ability was also examined (see Table 5, lower panel). Results of analyses including general cognitive ability showed that, consistent with WRRMP, there was evidence for generalist genetic overlap. A common genetic factor significantly accounted for variation in general cognitive ability, number sense, and math achievement (see significant loadings on a_1 in Table 5). However, there was also evidence of modest but significant residual genetic overlap between number sense and math that went beyond general cognitive ability ($a_2 = 0.19$ for math story problems and $a_2 = 0.21$ for math fluency). This finding differed from WRRMP, where no significant independent genetic effects were found between number sense and math after accounting for overlap with general cognitive ability. However, numerically, these results were in a similar range (math story problems: $a_2 = 0.25$; math fluency: $a_2 = 0.27$), but those values were not significantly different from zero. Like in WRRMP and the bivariate analyses, nonshared environmental factors were largely unique to each measure.

6. Discussion

The purpose of the present study was to examine the nature of the overlap among ANS acuity, mathematics, and general cognitive ability in two twin samples. We expanded upon traditional phenotypic analyses, which have suggested modest but significant overlap between ANS acuity and mathematics (Halberda & Feigenson, 2008; Schneider et al., 2017) in order to examine the etiology of this covariance. Across both samples, results suggested that individual differences in ANS acuity were due in part to significant additive genetic factors. This was consistent with twin findings of Tosto et al. (2014), which also found modest and significant genetic factors contributed to individual differences in ANS acuity in a larger twin sample. Expanding upon these univariate analyses, there was evidence that genetic factors associated with individual differences in ANS were shared with genetic factors that account for individual differences in mathematics. Though the correlation between ANS acuity and math may be modest, the results of the current study suggest that to the extent that they covary, the majority of this correlation is due to latent genetic factors shared by both traits. Moreover, when general cognitive ability was included in the models there was evidence of generalist genetic overlap among all three skills. Much of the overlap among all three traits was due to this general genetic overlap.

Genetic effects drive the relationship between ANS and mathematics

These trivariate results speak to the question of whether ANS should be conceived as a domain-specific cognitive precursor skill to later math outcomes in formal schooling. Our finding of general genetic influences was inconsistent with framing ANS as a purely domain-specific precursor to mathematics. These results suggest instead that the relationship between ANS and math is, in part driven, by generalist genetic factors that also contribute to domain-general cognitive skills.

Furthermore, the trivariate model can also be use to reconstruct the model-predicted correlation of ANS acuity and math after controlling for general cognitive ability, similar to the methods of Halberda et al. 2008, but in a way that takes into account the non-independence of twins as necessitated by the twin designs of the current studies. The phenotypic correlation between ANS and math controlling for general cognitive ability ranged 0.12 – 0.14. Across the studies, results were mixed as to whether this residual correlation reflected additional additive genetic influences specific to the relationship between ANS and mathematics, beyond factors shared with general cognitive ability. While the path representing overlap between ANS and mathematics beyond those effects accounted for by general cognitive ability was only significant in the trivariate analyses in the CLDRC sample, the magnitude of the estimate was similar across all four trivariate analyses (ranging 0.19 – 0.27). These divergent results between the samples suggest that we may be underpowered when examining unique genetic overlap of ANS and mathematics. However, the results suggest to the extent that ANS and math were correlated after partialling out general cognitive ability, this relationship was also largely due to shared genetic factors that are separable from general cognitive skills.

Notably, general cognitive ability was measured in two different ways across the two samples, with the g factor score in WRRMP being potentially more driven by verbal skills than the full scale IQ score in CLDRC. It is possible that a non-verbal math skill like ANS acuity would be more separable from verbal general cognitive skills than non-verbal general cognitive skills, though the current results did not fully bear that out. Further studies are needed to determine if there is indeed a small but significant set of unique genetic influences shared between ANS and mathematics. Thus, we found strong support for the proposal that generalist genes account for a portion of the overlap between ANS and mathematics and some evidence that ANS may have specific effects shared with mathematics above and beyond general cognitive skill. Moreover, these findings were largely the same across two math skills relevant to school math achievement – math story problem solving and math fact fluency.

Together, these genetic findings are inconsistent with the proposal of Tosto et al. 2014, that ANS is a fitness trait. The modest but significant heritability found in all three samples suggest that individual differences in ANS acuity are in, part genetic in origin. Moreover, the majority of the overlap of ANS and mathematics and general cognitive ability was due to genetic overlap, and there was no evidence of overlap due to nonshared environmental factors. This in turn suggests that the etiology of number sense is similar to many other cognitive traits with modest genetic influences. The overlapping confidence intervals on the univariate estimates of the contribution of additive genetics to ANS acuity compared to mathematics and general cognitive ability do not allow us conclude that ANS is less heritable than math and general cognitive skills. Our fairly wide confidence intervals suggest we were likely underpowered in comparing the magnitude of additive genetic variance across traits. Nonetheless, viewing ANS as a cognitive trait with etiology that functions much like many other cognitive traits is more compatible with the broader literature. Fitness traits, where heritability is predicted to be low, would be unlikely have the pattern of individual differences that ANS has in correlating with formal math achievement, a trait with moderate genetic influences, unless the majority of the overlap came from environmental factors. The results of the current study bring together two previously independent research streams – behavioral genetic and individual differences – into a more coherent understanding of ANS acuity and its influence on academic achievement.

Reliability and environmental influences

Moving beyond genetic findings, estimates for the nonshared environmental component of variance in ANS acuity were pronounced. This may be a concern because the nonshared environmental factor also includes measurement error and can be a sign of unreliability in the measure. There was no overlap of nonshared environmental influences associated with ANS acuity and either mathematics achievement or general cognitive ability. This suggests that nonshared environmental effects were unique to the ANS measure. The lack of nonshared environmental overlap further raises the concern that the large nonshared environmental estimates are an indicator of low reliability. Moreover, MZ correlations can be viewed as a lower bound of reliability. The MZ correlations in both samples were below 0.40, providing further evidence that high estimates for E may be a result of measurement unreliability and not large nonshared environmental impacts. Mazzocco, Feigenson, & Halberda (2011b) report a Cronbach's alpha of 0.65 for a slightly different version of the panamath task, partially corroborating this line of reasoning. This result is particularly problematic given that the standardized math scores have reliabilities often exceeding 0.90 (Woodcock, McGrew, & Mather, 2001). Low estimates of genetic variance previously reported (Tosto et al.,2014) and found in two samples in the current study, suggest an alternative interpretation to the proposal of Tosto et al. (2014) that ANS a fitness trait. Individual differences in ANS acuity likely have significant underlying genetic factors, which may be obscured by unreliability in the measure.

One factor contributing to interest in ANS is the possibility of training ANS acuity as a means to improve mathematical achievement (De Smedt et al., 2013; Feigenson, Libertus, & Halberda, 2013). Lack of environmental overlap may be on the surface concerning because educational experiences are often thought of as potentially identifiable sources of shared and nonshared environmental influence. However, the results of the current study do not suggest that gains made in ANS would be unlikely to transfer to math. Rather, results of the current study simply suggest that the current environments experienced by the twins in our samples, shared and nonshared, are not contributing significantly to individual differences. Further studies are warranted to investigate the genetic and environmental contributions to individual differences in ANS acuity in the presence of training.

Conclusion

The convergence across two twin samples adds confidence to the results, but the current study designs are not without their own limitations. Because of the differences in measurement across the two samples, the studies could not be combined. Both samples are relatively small, thus limiting our ability to produce tight confidence intervals around our estimates. In addition, the findings are limited to children in late childhood and early adolescence. A critical extension of the current research remains examining the etiology of these skills prior to formal schooling. Despite these limitations, the results of the current study bridges the gap between research into individual differences in ANS acuity in the mathematics literature and the etiology of ANS acuity in the behavioral genetics literature. Our results suggest that the etiology of ANS acuity functions like many other cognitive skills, as a moderately heritable trait that has genetic overlap with mathematics and general cognitive skills. ANS may have a small genetic contribution unique to its relationship with mathematics. However, the majority of the genetic influences that ANS acuity has on mathematics are accounted for by overlap with generalist genetic factors that contribute to individual differences in multiple cognitive traits.

Acknowledgments

The Western Reserve Reading and Math Project was supported by the Eunice Kennedy Shriver National Institute of Child Health and Development grants HD038075, HD059215, HD068728 and HD075460. The Colorado Learning Disability Research Center was supported by grant P50 HD027802. S. Lukowski is supported by the National Science Foundation Graduate Research Fellowship Program under grant no. DGE-1343012. M. Rosenberg-Lee is supported by a Career Development Award from the National Institute of Mental Health grant MH101394.

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Research Highlights

- Approximate number sense (ANS) has genetic overlap with mathematics
- Findings show generalist genetic overlap among ANS, math, and general cognitive ability
- The pattern of results suggest etiology of ANS acuity functions similar to math, *g*

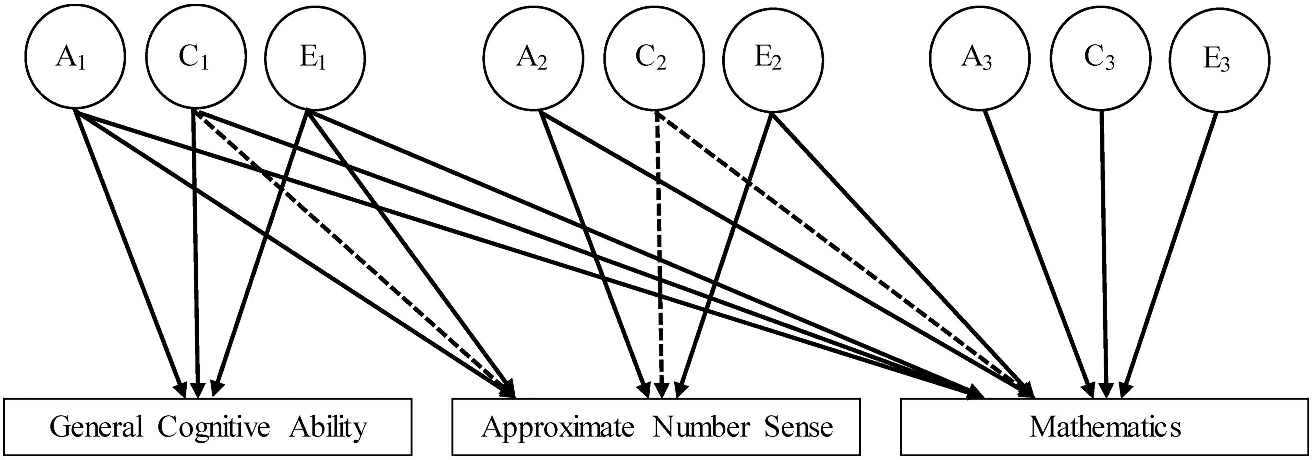

Figure 1.

Full Trivariate Model for the Western Reserve Reading and Math Project Sample. A represents additive genetic effects, C represents shared environmental effects, and E represent nonshared environmental effects. Dotted lines represent that the path was not estimated in the final model. In Colorado Learning Disabilities Research Center sample all paths from C were not estimated given the results of the univariate analyses.

Table 1

Descriptive statistics

Measure	Mean	Standard Deviation	Skew	Kurtosis
Western Reserve Reading and Math Project				
Panamath	0.34	0.25	−0.70	1.87
WJ III Applied Problems	106.37	11.80	−0.34	0.06
WJ III Math Fluency	100.22	16.22	0.35	−0.06
Colorado Learning Disabilities Research Center				
Panamath	0.26	0.16	−0.65	0.97
WJ III Applied Problems	108.92	10.58	−0.18	−0.31
WJ III Math Fluency	98.22	13.46	0.17	0.14

Note. Means and standard deviations are provided for the raw scores of the Panamath task and the standard scores of the Woodcock-Johnson Tests of Achievement (WJ III) tasks. Skew and kurtosis are provided for the distributions after sex, age, and months of schooling were regressed out. In addition, the Panamath variable was log transformed to better approximate a normal distribution.

Table 2

Phenotypic and intraclass correlations

Measure	**1**	**2**	**3**	**rMZ**	**rDZ**
Western Reserve Reading and Math Project					
1. Panamath	-			0.33[*]	0.08
2. WJ III Applied Problems	0.33[*]	-		0.75[*]	0.55[*]
3. WJ III Math Fluency	0.23[*]	0.49[*]	-	0.84[*]	0.50[*]
4. General Cognitive Ability	0.27[*]	0.65[*]	0.41[*]	0.77[*]	0.52[*]
Colorado Learning Disabilities Research Center					
1. Panamath	-			0.38[*]	0.09
2. WJ III Applied Problems	0.22[*]	-		0.84[*]	0.43[*]
3. WJ III Math Fluency	0.16[*]	0.48[*]	-	0.86[*]	0.31[*]
4. General Cognitive Ability	0.13[*]	0.63[*]	0.26[*]	0.83[*]	0.38[*]

Note.

[*] $p < 0.05$, WJ III = Woodcock Johnson Tests of Achievement III,

rMZ = intraclass correlation for monozygotic twins,

rDZ = intraclass correlation for dizygotic twins

Table 3

Univariate estimates for best fitting models

	A	C	E
Western Reserve Reading and Math Project			
Panamath	0.29* (0.13 – 0.43)	-	0.71* (0.57 – 0.87)
WJ III Applied Problems	0.39* (0.15 – 0.64)	0.36* (0.14 – 0.55)	0.25* (0.19 – 0.33)
WJ III Math Fluency	0.52* (0.31 – 0.76)	0.30* (0.06 – 0.49)	0.17* (0.13 – 0.24)
General Cognitive Ability	0.48* (0.23 – 0.77)	0.28* (0.01 – 0.49)	0.23* (0.18 – 0.32)
Colorado Learning Disabilities Research Center			
Panamath	0.54* (0.31 – 0.69)	-	0.46* (0.31 – 0.69)
WJ III Applied Problems	0.77* (0.67 – 0.84)	-	0.23* (0.16 – 0.33)
WJ III Math Fluency	0.82* (0.54 – 0.88)	-	0.18* (0.12 – 0.27)
General Cognitive Ability	0.86* (0.82 – 0.90)	-	0.14* (0.11 – 0.18)

Note.

$^{*}p < 0.05$, WJ III = Woodcock Johnson Tests of Achievement III

Table 4

Bivariate estimates for the overlap of ANS and mathematics

	a_1	a_2	c_2	e_1	e_2
Western Reserve Reading and Math Project					
Panamath	0.56*(0.41 – 0.67)			0.83*(0.74 – 0.91)	
WJ III Applied Problems	0.58*(0.40 – 0.72)	0.12 (0.00 – 0.55)	0.63*(0.45 – 0.73)	0.02 (0.00 – 0.11)	0.50*(0.43 – 0.57)
Panamath	0.54*(0.37 – 0.66)			0.84*(0.75 – 0.93)	
WJ III Math Fluency	0.35*(0.15 – 0.57)	0.65*(0.38 – 0.83)	0.53*(0.21 – 0.69)	0.02 (0.00 – 0.10)	0.42*(0.37 – 0.49)
Colorado Learning Disabilities Research Center					
Panamath	0.72*(0.52 – 0.83)			0.69*(0.57 – 0.86)	
WJ III Applied Problems	0.34*(0.15 – 0.55)	0.81*(0.68 – 0.88)	-	0.00 (0.00 – 0.09)	0.48*(0.40 – 0.57)
Panamath	0.72*(0.51 – 0.82)			0.70*(0.57 – 0.86)	
WJ III Math Fluency	0.26*(0.06 – 0.48)	0.87*(0.76 – 0.92)	-	0.00 (0.00 – 0.07)	0.43*(0.36 – 0.53)

Note.

* $p < 0.05$, WJ III = Woodcock Johnson Tests of Achievement III

Table 5

Trivariate estimates examining overlap with general cognitive ability

Measure	a_1	a_2	a_3	c_1	c_3	e_1	e_2	e_3
Western Reserve Reading and Math Project								
g	0.70* (0.50 – 0.87)			0.52* (0.17, 0.69)		0.48* (0.42 – 0.56)		
Panamath	0.41* (0.26 – 0.60)	0.39 (0.00 – 0.56)		-		0.00 (0.00 – 0.12)	0.83* (0.74 – 0.91)	
WJ III Applied Problems	0.53* (0.31 – 0.73)	0.25 (0.00 – 0.51)	0.00 (0.00 – 0.45)	0.47* (0.18, 0.71)	0.43 (0.00 – 0.54)	0.09 (0.00 – 0.20)	0.03 (0.00 – 0.12)	0.49* (0.43 – 0.55)
g	0.69* (0.49 – 0.87)			0.53* (0.18, 0.70)		0.48* (0.42 – 0.56)		
Panamath	0.40* (0.24 – 0.60)	0.38 (0.00 – 0.56)		-		0.00 (0.00, 0.16)	0.83* (0.75 – 0.92)	
WJ III Math Fluency	0.23 (0.00 – 0.47)	0.27 (0.00 – 0.83)	0.67 (0.00 – 0.84)	0.36* (0.01, 0.64)	0.34 (0.00 – 0.58)	0.14* (0.06 – 0.22)	0.02 (0.00 – 0.09)	0.39* (0.34 – 0.45)
Colorado Learning Disabilities Research Center								
g	0.93* (0.91 – 0.95)			-		0.37* (0.32 – 0.42)		
Panamath	0.15* (0.02 – 0.27)	0.71* (0.49 – 0.82)		-		0.00 (0.00 – 0.07)	0.69* (0.57 – 0.86)	
WJ III Applied Problems	0.66* (0.58 – 0.72)	0.19* (0.03 – 0.34)	0.56* (0.46 – 0.64)	-	-	0.12* (0.01 – 0.23)	0.00 (0.00 – 0.12)	0.46* (0.39 – 0.54)
g	0.93* (0.91 – 0.95)			-		0.37* (0.32 – 0.42)		
Panamath	0.15* (0.02 – 0.27)	0.69* (0.47 – 0.81)		-		0.00 (0.00, 0.07)	0.70* (0.57 – 0.87)	
WJ III Math Fluency	0.31* (0.17 – 0.42)	0.21* (0.01 – 0.42)	0.83* (0.73 – 0.89)	-	-	0.01 (0.00 – 0.12)	0.00 (0.00 – 0.08)	0.43* (0.35 – 0.52)

Note.

* $p < 0.05$, WJ III = Woodcock Johnson Tests of Achievement III