

Genetics and the Evolution of Language: What genetic studies reveal about the evolution of language

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Abstract. In this paper I argue that genetic studies of language provide insights about the evolution of language. The finding that genetic factors affect all aspects of language is consistent with theories that argue that language is at least partially the result of innate factors, and that the factors have evolved. Genetic factors appear to play a greater role for syntax and phonology than for the lexicon, suggesting that the evolutionary history of syntax and phonology differs from that of the lexicon. Genetic factors also affect the linguistic abilities of language-impaired children more than normal children, consistent with the evolutionary history of language in language-impaired and normal children being different. The high degree of genetic overlap for linguistic abilities and oral motor and fine motor abilities is consistent with evolutionary theories that argue that complex fine motor skills and non-linguistic oral motor skills were the precursors to language. Similarly, the high degree of genetic overlap for linguistic and social ability suggests that aspects of language could have evolved from social abilities. The greater genetic overlap for syntax and phonology than for either the lexicon and syntax or the lexicon and phonology suggests that the evolutionary history of syntax and phonology is more similar than that of the lexicon and either syntax or phonology. Taken as a whole, these genetic findings are most consistent with linguistic models and evolutionary theories of language that invoke both general and language-specific factors.

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In this paper, I will discuss how genetic studies of language can inform discussions about the evolution of language. Depending on the results of genetic studies, the answer could be that genetic studies have *nothing* to add to such discussions. I take a more optimistic view and argue that genetic studies *can* and *do* provide insights about the evolution of language. The organization of this paper is as follows. I begin with a brief discussion of the relationship between genetics and the evolution of language, outlining some of the assumptions and limitations that exist about their relationship. I then briefly summarize findings of published behavioral studies and our ongoing twin study of language. I end with a brief description of current theories about the evolution of language, discussing how results from genetic studies can inform and constrain theories about how human language evolved.

1. The relationship between genetics and the evolution of language

1.1 Linguistic variability and the role of genetic factors. If language is heritable, this suggests that genetic factors play a role in language acquisition and/or the linguistic proficiency that people attain. It is logically possible that genetic factors affect the rate at which children acquire language, but that all people eventually attain the same linguistic proficiency, albeit at different ages. If this is the case, we would expect substantial heritability for the linguistic abilities of children, but not for adults. If all people have the same linguistic abilities by the time they reach sexual maturity, the lack of phenotypic differences among adults means that linguistic ability could not be selected for, unless children's linguistic abilities affect the probability they will survive to adulthood.

Results of some studies indicate that language acquisition *does* vary among children. Although the course of acquisition is remarkably similar for all children acquiring a given language (for a summary, see Stromswold, 2000), some children learn language more rapidly than others. For example, some normal 24-month old English-speaking children say only a handful of words, whereas others say over 300 words (e.g. Fenson et al., 1994; Goldfield & Reznick, 1990). Brown (1973) and Cazden (1968) investigated when 3 English-speaking children acquired 14 grammatical morphemes, and found that, although all 3 children acquired these morphemes in the same order, the children acquired them at different ages. For example, all 3 children mastered the third person singular verbal inflection *-s* after they had mastered the homophonous plural and possessive morphemes, but one child mastered the *-s* verbal inflection at 2 years, 3 months (2;3), whereas the other two children did not achieve mastery until ages 3;6 and 3;8. Similar differences in the rate of acquisition have been reported for questions

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(Stromswold, 1988, 1995), auxiliary verbs (Stromswold, 1989, 1990), and datives, verbal particles and related constructions (Snyder & Stromswold, 1997; Stromswold & Snyder, 1995).

It is also logically possible that all children acquire language at the same rate, but that as adults, they differ in their linguistic abilities. It is possible, for example, that whereas all children acquire the same basic competence in their language, at a certain age the linguistic development of some children stagnates where the linguistic development of other children continues. This is most plausible (and indeed is likely) with respect to vocabulary acquisition. Clearly, adults differ in the size of their vocabularies, and this may reflect the fact that some people regularly acquire new vocabulary items as adults, whereas the vocabularies of other people fossilize. It is also possible that adults have different grammatical knowledge (competence) or performance. For example, all normal adults may acquire the basic morphosyntax of their language, but only some adults master the morphosyntax of rare linguistic constructions (e.g., the English subjunctive, *if I were a plant, I would have chlorophyll rather than hemoglobin*). It is also possible that all adults have the same grammatical competence, but performance factors (such as short term memory size) affect the ease with which adults produce and perceive language. Given that what could potentially be selected for is observable phenotypes (in this case linguistic performance) rather than unobserved differences in underlying competence, what is important from an evolutionary standpoint is that adults differ in linguistic performance rather than in the underlying linguistic ability that linguists are typically interested in. Furthermore, even if adults' linguistic performance differs, it is possible that these differences do not affect reproductive success, just as eye color presumably does not affect reproductive success. In other words, even if we find significant heritabilities for adults' linguistic abilities, it might tell us nothing about the evolution of language.

Some studies suggest that, although all normal adults have a basic level of linguistic competence in their native language, some adults are more linguistically adept than others. For example, individual differences have been reported in verbal fluency (Day, 1979), in the interpretation of novel compound nouns (Gleitman & Gleitman, 1970), in sentence processing (Bever, Carrithers, Cowart, & Townsend, 1989; Just & Carpenter, 1992), and in the ability to acquire a second language as an adult (Fillmore, 1979). Even among native adult speakers of the same dialect, there are individual differences in grammaticality judgments (Cowart, 1997; Nagata, 1992; Ross, 1979; Schutze, 1996).

1.2 The role of genetics in language-impaired and linguistically normal people. It is possible that genetic factors play a role in the acquisition of language and the linguistic proficiency of language-impaired people, but genetic factors play no role for people who are not language-impaired (henceforth, normal people). If this is the case, it suggests that different genetic factors affect the linguistic abilities of language-impaired and normal people. Even if the same genetic factors are involved, if genetic factors play a substantially greater role for language-impaired than normal people, this suggests that there the populations may be genetically distinct from one another.

1.3 Heritability Estimates and Linguistic Variability. Heritability (h^2) is an estimate of the extent to which genetic factors account for the observed (phenotypic) variance in a trait. If people do not vary in linguistic ability, then the heritability estimate for language will be zero, even if genetic factors are completely responsible for human language. If there is significant heritability for language, this means that the linguistic abilities of people differ *today* and genetic factors account for a non-negligible amount of the variance. As discussed above, if there is genetically-determined variance in people's linguistic abilities, this means that something that

contributes to linguistic ability *could* have been selected for. It does not, however, mean that any linguistically-related ability *was* selected for. Furthermore, even if some language-related ability was selected for, it does not say *what* was selected for. It could be, for example, that the ability was not specifically linguistic, but rather affected both linguistic and nonlinguistic abilities. It is also possible that there are genetic factors that selectively affect linguistic ability, but the same genetic factors affect all aspects of language (e.g., phonology, the lexicon, and syntax).

1.4 Genetic Overlap of Linguistic and Nonlinguistic Abilities. Thus, one way genetic studies of language can inform theories about the evolution of language is by investigating the extent to which the genetic factors that affect language also affect other abilities. If we find that the genetic factors that affect linguistic ability (or some aspect of linguistic ability) also affect nonlinguistic abilities (or a particular nonlinguistic ability), this is *consistent* with linguistic and nonlinguistic abilities having shared neural underpinnings and/or evolutionary history. For example, if there is substantial genetic overlap between oral motor abilities and the ability to speak clearly, this suggests that these abilities have some component skill(s) in common. In this example, *a priori*, a very plausible skill that underlies nonlinguistic oral motor abilities and articulation is the ability to produce rapid, complex oral movements. It is plausible that aspects of the brain have evolved to allow for the efficient and accurate production of both linguistic and nonlinguistic oral movements. Similarly, to the extent that we find genetic overlap for subcomponents of language (e.g., syntax and phonology), this suggests overlap in the neural circuitry that subserve these aspects of language, which in turn suggests that these subcomponents of language could have co-evolved. However, in neither case does the existence of genetic overlap between different abilities *prove* that the abilities share neural circuitry or evolutionary history. It could just be happenstance.

2. Previous twin studies

2.1 The logic of twin studies. We can't tell whether individual differences in language acquisition and linguistic ability discussed in section 1.1 are the result of environmental and/or genetic factors, but the fact that such differences exist suggests that people may differ in their genetic endowments for language. The most common method used to tease apart the role of genetic and environmental factors in language is to determine whether MZ cotwins are linguistically more similar to one another than DZ cotwins. Because MZ and DZ cotwins share essentially the same pre- and postnatal environments, whereas MZ cotwins share 100% of their alleles and DZ cotwins share only 50% of their alleles (but see Stromswold, 2001; Stromswold, to appear), if MZ cotwins are linguistically more similar to one another than DZ cotwins, this suggests that genetic factors play a role in language. If, on the other hand, MZ cotwins are no more similar to one another than DZ cotwins, this suggests that genetic factors play a negligible role for language. Putting aside for the moment the possibility of interactions and correlations between genetic and environmental factors (but see Stromswold, 2005), the variability in linguistic abilities in a population (the phenotypic variance) is due to genetic variance plus environmental variance. Heritability is a measure of the proportion of the phenotypic variance that is due to genetic variance. In twin studies, environmental factors that may contribute to phenotypic variance are divided into those environmental factors that co-twins do and do not share. Shared environmental factors include the linguistic input children receive (assuming parents of twins speak the same way to both cotwins), and nonshared environmental factors include illnesses or accidents that only occur to one cotwin.

2.2 Concordance rates for language disorders. One way to determine whether MZ cotwins are linguistically more similar than DZ cotwins is to compare the MZ and DZ concordance rates for language disorders. Twins are concordant for a language disorder if both cotwins are impaired, and discordant if only one cotwin is impaired. If the concordance rate for language disorders is significantly greater for MZ than DZ twins, this suggests that genetic factors play a role in language disorders such as dyslexia and specific language impairment (SLI). Stromswold (2001) performed meta-analyses of 10 twin studies of written or spoken language disorders. In these 10 studies, the mean concordance rate was 80% for MZ twins and 46% for DZ twins. In all 10 studies, concordance rates were greater for MZ than DZ twin pairs, with the differences being significant in all but one study. When the twin pairs from the studies were pooled together, the overall concordance rate was significantly higher for MZ twins (80%) than DZ twins (46%). In the 5 twin studies of written language disorders, the mean concordance rate was 76% for MZ twins and 41% for DZ twins, with the overall concordance rate for MZ twins (75%) being significantly greater than for DZ twins (43%). For the 5 twin studies of spoken language disorders, the mean concordance rate was 84% for MZ twins and 52% for DZ twins, with the overall concordance rate for MZ twins (84%) being significantly greater than for DZ twins (50%). One can obtain an estimate of the role of heritable factors for a disorder by doubling the difference in MZ and DZ concordance rates for the disorder. For example, given that the concordance rate for spoken language impairments is 84% for MZ twins and 50% for DZ twins, the heritability of spoken language impairments is 68%. An estimate of the role of shared environmental factors can be obtained by subtracting the heritability estimate from the MZ concordance rate ($84\% - 68\% = 16\%$), and an estimate of the role of non-shared environmental factors can be obtained by subtracting the MZ concordance rate from 100 (here 16%).

Heritability estimates that are based on concordance analyses have a number of limitations. First, they are only as valid as the diagnoses given to twins. If even a small percentage of non-impaired twins are (incorrectly) diagnosed as being language impaired or if some language-impaired twins are incorrectly deemed to be normal, this can dramatically affect heritability estimates. Secondly, the estimates are only as specific as the diagnoses twins receive. If (some of) the twins' linguistic impairments are secondary to non-linguistic deficits, then the estimates obtained will not be good estimates of the heritability of linguistically-specific impairments. A third limitation of heritability estimates obtained from twin concordance analyses is that they are estimates of broad-sense heritability, and as such include the influence of gene dominance, epistasis (interactions between genes) and interactions between genes and environment.

2.3 Univariate analyses of twins' linguistic abilities. There are two additional drawbacks that are fairly specific to concordance-based heritability estimates. The first drawback has to do with the fact that concordance analyses take what is likely to be a continuous variable (linguistic ability) and artificially categorize people as either impaired or not impaired. Inevitably, there will be cases in which one twin scores just a few points higher than his or her cotwin, but this small difference is enough for one twin be labeled normal and the other impaired. The second drawback is that twin concordance studies can only be used to study the heritability of language impairments, and not the heritability of normal linguistic function. This is important because it is becoming increasingly clear that there isn't perfect overlap in heritable factors that affect language development and proficiency in people who have normal language versus impaired language (see Stromswold, 2001). In cases where the data obtained are more or less continuous (e.g., scores on language tests, age of acquisition of linguistic milestones) rather than dichotomous (presence or absence of a language disorder), one can address both of these

drawback by comparing the similarity of normal MZ and DZ cotwins' language scores.

In univariate analyses, a twin's performance on test A is compared with his cotwin's performance on the same test. In meta-analyses of 8 studies of normal twins' vocabulary development, Stromswold (2001) found that the mean weighted correlation coefficient was .93 for MZ twins (as compared to .76 for DZ twins). For phonemic awareness, the MZ correlation coefficient was .90 (compared to .56 for DZ twins). For articulation, the correlation coefficient was .92 for MZ twins and .85 for DZ twins. For reading, the coefficient for MZ twins was .86 (as compared to .66 for DZ twins), and for spelling, the coefficient was .78 for MZ twins (as compared to .48 for DZ twins). Stromswold (2001) reported the results of 12 twin studies in which 36 tests of morphosyntax were administered. Unfortunately, the variability among these tests precluded calculating mean correlation coefficients. However, Stromswold (2001) noted that in 33 of the 36 tests, the MZ correlation coefficient was larger than the DZ correlation coefficient, with the difference being significant for 12 of the 36 morphosyntactic tests. One can obtain estimates of the effect of heritable factors by comparing the similarity of MZ and DZ cotwins' scores on a test. For example, Falconer's (1960) heritability estimate is calculated by doubling the difference between the MZ and DZ intra-twin correlation coefficients. The role of shared environmental factors is computed by subtracting Falconer's heritability estimate from the MZ correlation coefficient, and the role of non-shared environmental factors is calculated by subtracting the MZ correlation from one. We can use these formulas to estimate, for example, that 68% of phonemic awareness is due to heritable factors, 22% is due to shared environmental factors, and 10% is due to nonshared environmental factors. Univariate analyses clearly reveal that for a wide range of linguistic tasks, normal MZ cotwins perform more similarly to one another than DZ cotwins do. This suggests that heritable factors play a substantial role in the linguistic abilities of normal people. However, like heritability estimates based on twin concordancy, Falconer's heritability estimates are estimates of broad sense heritability. A second limitation of univariate twin analyses is that they do not allow one to tell whether the heritable factors that affect language are specific to language. It is possible, for example, that the heritable factors that affect phonemic awareness also influence other cognitive, linguistic or motor abilities.

Twin data can also be analyzed using structural equation modeling (SEM) techniques.² The underlying assumption of SEM analyses is that variance of a quantitative phenotype can be broken down into genotypic variance and environmental variance. Genotypic variance can be subdivided further into variance due to additive genetic effects (A) and variance due to non-additive or dominant (D) genetic effects (Neale & Cardon, 1992). Additive genetic effects are the effects of genes taken singly and added over multiple loci, whereas non-additive genetic effects are the effects of intralocus gene interactions. Environmental factors can be divided into environmental factors shared by co twins (C) and factors not shared by cotwins (E). Shared environmental effects contribute to cotwins' phenotypic similarity and non-shared environmental effects contribute to cotwins' dissimilarity. Models are formed by the weighted combinations of the parameters A, C, D, and E, with possible models being ACE, ADE, AE, CE, and E. Goodness of fit and degrees of freedom are the criteria used to determine which model provides the best fit to the data (Neale & Cardon, 1992).

² There are two reasons why SEM analyses were not performed on the meta-analytic twin data. First, in all but a handful of studies, the published reports of studies did not provide enough information to allow one to perform SEM analyses of the data from that study.

2.4 Multivariate analyses of twins' linguistic abilities. Multivariate analyses can help determine how specific-to-language the genetic factors that influence language are (see de Jong, 1999). In bivariate analyses, a twin's performance on test A is compared with his cotwin's performance on test B. Genetic influence on the phenotypic correlation between test A and B (bivariate heritability, h_b^2) is estimated by determining the extent to which the MZ cross-twin correlation is greater than the DZ cross-twin correlation. In contrast, the genetic correlation (R_G) estimates the extent to which the same genetic factors affect A and B regardless of their contribution to the correlation between A and B. Genetic correlation may be high, yet bivariate heritability low and vice versa. For example, genetic factors might play a substantial role for both gross motor abilities and linguistic abilities, but if completely different genetic factors are responsible for gross motor and linguistic abilities, the genetic correlation will be zero. Conversely, genetic factors might play only a modest role for gross motor and linguistic abilities, but if the same genetic factors are responsible for both abilities, the genetic correlation will be high.

One limitation of multivariate analyses is that estimates of the genetic correlation for two behavioral traits are only as good as the behavioral tests used to assess the two traits. For example, analyses of the Twins Early Development Study (TEDS) data suggest that the same genes affect vocabulary development and syntactic development, and that no vocabulary- or syntax-specific genetic factors exist (Dale, Dionne, Eley, & Plomin, 2000). However, this might reflect limitations in the way syntactic and lexical development were assessed. In the TEDS study, parents assessed their twins' lexicons by indicating whether they said each of 100 words. Parents then assessed their twins' syntax by choosing which sentence in 12 pairs of sentences (e.g. baby crying, baby is crying) sounded more like something that their twins might say. It seems plausible that, during the early stages of language learning, parents are fairly good at recalling whether their child says particular words and, hence, that the TEDS vocabulary measure is probably a reasonable measure of lexical development. The same is not necessarily true of the TEDS syntax measure. It is very unlikely that a child has said the exact sentences listed, so to complete the syntax measure, parents must act as amateur developmental linguists. Furthermore, parents complete the syntax section immediately after completing the vocabulary checklist. Therefore, one worry is that parents who check off many words on the vocabulary test might (unconsciously) be biased to choose the "better" of the sentences in each pair, whereas parents who check off few words might be biased to choose the "worse" sentence in each pair. If such a bias exists, it would explain the high R_G for vocabulary and syntax.

A second limitation of multivariate analyses is that they only allow one to determine the extent to which there is genetic overlap for the particular behavioral traits that one has assessed. For example, researchers involved in the TEDS study have used multivariate analyses to determine the specificity of genes that affect verbal and nonverbal abilities. In addition to heritable factors that influence both nonverbal cognitive abilities and verbal abilities, there appear to be genetic factors that influence verbal abilities but not nonverbal cognitive abilities (e.g., Price et al., 2000). It is possible, however, that these latter genetic factors affect more than just verbal abilities. For example, genetic factors that affect verbal abilities but not nonverbal cognitive abilities could nonetheless affect oral motor abilities, fine motor abilities, gross motor abilities, social-emotional abilities, etc.. The only way to rule this out is to assess all of these abilities in the same group of subjects, and perform the appropriate analyses. Unfortunately, in order to have the statistical power to do so, one must have data from a very large number of twins.

3. *The Perinatal Environment and Genetic Interaction (PEGI) study*

3.1 Overview. In 2002, we began a behavior genetic twin study that investigates how genetic and prenatal and postnatal environmental factors affect linguistic and nonlinguistic development. This study is unusual in two ways. First, we have data on a wide range of the twins' linguistic development (phonological, lexical and syntactic) and nonlinguistic development (cognitive, gross motor, fine motor, oral motor, and social). Second, we have extensive information about our twins' prenatal and perinatal periods. The results alluded to in this paper are those obtained from the first 260-odd same-sex twin pairs who were between the ages of 2 and 6 when they were evaluated. It is clearly beyond the scope or goals of this paper to present in detail the analyses performed or the results obtained. Rather, we only summarize those findings that we believe are most likely to inform evolutionary theories of language. (For a more detailed description of the PEGI study and its findings, see Stromswold, 2005; Stromswold, Schramm, Molnar, Holodak, & Sheffield, 2005)

3.2 Measures of Linguistic and Nonlinguistic Abilities. The PEGI twins' linguistic and nonlinguistic abilities were assessed in a variety of ways. First, the twins' linguistic abilities were assessed using the parent-administered Ages and Stages (AS) communication test (Bricker & Squires, 1999). The linguistic abilities of twins who were under 3 years old were also assessed using the age-appropriate version of the parent-completed MacArthur Communication Development Inventory (CDI) vocabulary and syntax checklists described in section 2.4 (Dale, 2001; Fenson et al., 1994). The linguistic abilities of twins who were between 3 and 6 years old were assessed using the age-appropriate version of the Parent Assessment of Language (PAL, Stromswold, 2003) articulation, vocabulary, and syntax tests. The PAL articulation test is a test in which children are asked to imitate the onset of 12 words. The vocabulary test is a lexical access test in which children are asked to name as quickly as possible examples of a specified category (e.g., name as many animals as you can). The syntax test is a 12 item forced-choice picture-pointing comprehension test of semantically reversible active sentences, passive sentences, and sentences that contain reflexive pronouns (e.g., *himself*) or accusative pronouns (e.g., *him*). We also asked parents to report when their twins acquired 4 linguistic milestones (onset of babbling, first words, first multiword utterances, and clear articulation). Lastly, we asked parents to report whether their twins received speech-language therapy during each year of the twin's life. In addition to these linguistic measures, the PEGI study also includes 7 gross motor measures (AS gross motor score, amount of physical therapy received, and onset of sitting, crawling, walking, running, and climbing stairs), 5 fine motor measures (AS fine motor scores, amount of occupational therapy received, and onset of finger feeding, fork feeding and scribbling, 2 oral motor measures (amount of feeding therapy received and onset of drinking from an open cup), 3 social measures (AS personal-social scores, onset of social smiling, and amount of psychological or behavioral therapy), and 2 cognitive measures (AS problem solving scores and amount of special educational services received). (All measures may be found at http://rucss.rutgers.edu/~karin/PERINATAL/language_perinatal.htm.)

3.4 Genetic factors in the language of language-impaired and normal twins. We identified those twin pairs in which one or both twins were language-impaired.³ Concordance

³ Twins were classified as language-impaired if a speech therapist had diagnosed them as being language-impaired, or if they had received 2 or more years of speech-language therapy.

analyses of these twin pairs revealed that genetic factors accounted for over 80% of the language disorders in our twins. In addition, structural equation modeling (SEM) analyses revealed that genetic factors accounted for more of the linguistic variance for the language-impaired twins than for the normal twins. For example, non-additive (i.e., dominant) genetic factors only played a role in the linguistic abilities of language-impaired twins. That said, for both language-impaired twins and normal twins, the same general pattern was found with genetic factors playing a greater role for articulation (70% and 31% respectively for language-impaired and normal twins) and syntax (100% and 26% respectively for language-impaired and normal twins) than for vocabulary (69% and 5%, respectively for language-impaired and normal twins).

3.5 Heritability of Linguistic Abilities. Because we found the same basic pattern of results for the language-impaired and normal twins, we combined all of the twins into a single group for further analyses. Doing so allowed us to examine the degree of genetic overlap between linguistic and nonlinguistic abilities.⁴ For all subcomponents of language, genetic factors accounted for a significant percentage of twins' abilities. Not surprisingly, the findings for all twins were somewhere between the results obtained for language-impaired twin pairs and normal twin pairs. For vocabulary, genetic factors accounted for only 18% of twins' abilities, whereas genetic factors accounted for 41% of their phonological abilities and 60% of their syntax abilities.

3.6 Heritability of Nonlinguistic Abilities. When nonlinguistic data from language-impaired twins and normal twins were combined, genetic factors accounted for a substantial portion of the variance for most of the nonlinguistic abilities studied, with genetic factors accounting for approximately a third of twins' fine motor abilities, approximately half of their social abilities, approximately two-thirds of their gross motor abilities and essentially all of their cognitive abilities. Indeed, nonlinguistic oral motor ability was the only nonlinguistic ability for which genetic factors did not play a substantial role. In post hoc analyses, we found that genetic factors played a greater role in the nonlinguistic abilities of language-impaired twins than normal twins. This raises the possibility that, for at least a subset of the language-impaired twins, the language impairment is not a linguistically specific, but rather is secondary to a more general impairment.

3.7 Genetic overlap for linguistic and nonlinguistic abilities. When we investigated the genetic overlap for linguistic and nonlinguistic abilities for all twins, we found that the genetic overlap between linguistic and nonlinguistic ability varied according to the nonlinguistic ability considered. The genetic overlap was greatest for oral motor and linguistic abilities (more than 90% overlap for therapy measures) and fine motor and linguistic abilities (approximately 80% overlap for AS scores and 90% overlap for therapy measures) followed by social and linguistic abilities (approximately three-quarters genetic overlap for AS scores and one-half overlap for therapy measures) followed by cognitive and linguistic abilities (approximately one-half overlap for AS scores and one-quarter overlap for therapy measures⁵), with considerably less genetic

⁴ Ideally, we would have determined the overlap of linguistic and nonlinguistic abilities of language-impaired twins and normal twins separately. Alas, we only had adequate statistical power to perform bivariate analyses when data from all the twins were included in the analyses.

⁵ The genetic overlap between speech-language therapy and special education services should be interpreted with caution, as most of the twins in the PEGI study were not yet school-age. Because special education services are usually provided in a school setting, most of the twins were too young to have received special education services.

overlap between gross motor and linguistic abilities (approximately 10% for AS scores and 50% for therapy measures).

It is intriguing that the genetic overlap between linguistic and nonlinguistic abilities was particularly high for oral motor and fine motor abilities. One interpretation of these results is that they reflect shared neural circuitry for tasks that require complex motor control (perhaps involving the recruitment of supplementary motor area). The overlap between language and social ability is also intriguing. One possibility is that this overlap reflects shared neural circuitry for social skills and social-pragmatic aspects of language. Indeed, this explanation is consistent with the results of post hoc analyses that revealed little genetic overlap between our measures of social skill and our measures of formal aspects of language (specifically, PAL phonology and syntax scores).

3.8 Genetic overlap for linguistic milestones. When we investigated the genetic overlap for age of acquisition of linguistic milestones, we find considerable genetic overlap for the onset of words and multiword utterances, the onset of words and clear articulation, and the onset of multiword utterances and clear articulation. In striking contrast, there was essentially no genetic overlap between the onset of babbling and any of the other three linguistic milestones. This suggests that different genetic factors may be involved in babbling than in the production of words, sentences and clearly articulated sentences. Indeed, it is possible that contrary to common belief, babbling is not a precursor to linguistic communication. Furthermore, if we are correct that different genetic factors affect babbling, this could mean that the evolutionary history of babbling may be different from that of other aspects of language.

3.9 Genetic overlap for parent-report measures of lexical and syntactic development. When we look at the genetic overlap for our two parent-report measures of the lexicon and syntax (the CDI vocabulary and sentence structure scores and the word and sentence milestone measures), we find almost complete genetic overlap. Although this could reflect some deep underlying property of words and sentences, we think two other possibilities are more likely. The first possibility is that the genetic overlap for words and sentences merely reflects that these measures are expressive measures. Indeed, this explanation is consistent with our observation that there is considerable genetic overlap for the clear articulation milestone and both the word and sentence milestones. However, our results for the PAL measures of lexical and syntactic ability suggest that this is not the correct explanation (see section 3.9). The second possible explanation is that the genetic overlap reflects the fact that CDI and milestone measures are parent-report measures. As discussed in section 2.4, this may well account for the genetic overlap between CDI word and sentence measures. We suspect that the word and sentence milestone measures may also suffer from the same basic problem: if parents remember that their child said his or her first word at an early age but they can't remember exactly when the child first began saying sentences, they may assume (or erroneously recall) that s/he began producing sentences at an earlier age than s/he actually did. This explanation would also account for the considerable genetic overlap for the word, sentence and clear articulation milestones.

3.10. Genetic overlap for phonology, lexical, and syntactic PAL test scores. Recall that the PAL phonology and lexical tests require that children produce speech (i.e., they are expressive measures), whereas the PAL syntax test is a comprehension test. Thus, if the genetic overlap between CDI word and sentence scores and between word and sentence milestones are due to these measures being expressive, we would predict greater genetic overlap for phonology and lexical PAL scores than for syntax PAL scores and either phonology or lexical PAL scores. Contrary to this prediction, we found greater genetic overlap for syntax and phonology scores

than for lexical scores and either syntax or articulation scores.

What accounts for the substantial genetic overlap for syntax and phonology? Hauser, Fitch and Chomsky (2002) argue that recursion is the only property that is specific to human language (i.e., what they refer to as the Faculty of Language Narrow, FLN). If syntax is recursive but phonology is not (as claimed by Hauser et al., 2002), the genetic overlap between phonology and syntax cannot be a reflection of recursion. There are two ways of dealing with this. The first is to argue that Hauser, Fitch and Chomsky (2002) are wrong and phonology is, in some sense, recursive. The second is to argue that some other property is shared by phonology and syntax. Depending on whether this property is specific to human language (i.e., a property that is not shared with any other nonlinguistic human ability or with any ability of any non-human species), this property would be part of FLN or the broader set of abilities that are required for human language (what Hauser et al., 2002 refer to as the Faculty of Language Broad, FLB).

Although we cannot know for sure, phonology and syntax share (at least) two properties that could account for their large genetic overlap. The first has to do with the combinatoric nature of phonology and syntax. In both phonology and syntax, simple units combine together to form more complex units. In the case of phonology, the units are phonemes that combine to form syllables.⁶ In syntax, words (or more precisely, morphemes) combine to form sentences (or more precisely, clauses). Thus, one possible explanation for the genetic overlap between syntax and phonology is that this overlap reflects the combinatoric nature of these aspect of language. If this is the correct explanation for the genetic overlap between syntax and phonology, we would predict that if we tested children on their ability to produce and/or comprehend derivational complex words (e.g., *teach+er*, *bird+bath*), we would find the genetic overlap between derivational morphology and syntax to be at least as great as the overlap between phonology and syntax.⁷

The second possible explanation for the genetic overlap between syntax and phonology is that phonology and syntax both have hierarchical, branching structures with higher nodes dominating intermediate nodes that in turn dominate the atomic elements. In the case of phonology, the highest node in the hierarchy is the syllable, the intermediate nodes in the hierarchy are onsets and rimes. Rimes in turn are composed of nuclei and codas, and onsets, nuclei and codas are all composed of phonemes. In syntax, lexical and grammatical morphemes combine to form phrases that in turn combine to form clauses that combine to form sentences.

Phonological and syntax units are constrained in the ways in which they can be combined, and these constraints make reference to the hierarchical structure of phonology and syntax. To take a trivial example, in a syllable, the onset and coda may be null, but the nucleus cannot. In other words, all syllables must contain a vowel. Further phonological constraints appear to exist across languages (e.g., the sonority hierarchy) and within languages. For example, within a language, although an onset may be comprised of more than one consonant

⁶ The atomic elements could also be phonetic features (i.e., phonemes could be comprised of phonetic features like voicing). Either way, the logic is the same.

⁷ In many, but not all, linguistic theories, inflectional morphology (e.g., the *-ing* and *-ed* in *walk-ing* and *walk-ed*) is considered part of syntax. Such theories would predict substantial genetic overlap between inflectional morphology and syntax because both tap syntactic abilities. Indeed, in terms of genetic overlap, according to theories that combine inflectional morphology and syntax (e.g., Chomsky's Minimalist Program, Chomsky, 1992/1993), we should find greater overlap between syntax and inflectional morphology than between syntax and phonology.

(i.e., an onset may be a consonant cluster), there are restrictions on *which* phonemes can form clusters and the order in which these phonemes must occur. For example, in English /st/ is a legitimate consonant cluster in onset position, but /St/ is not. Furthermore, /st/ is allowed, but /ts/ is not. Lastly, certain consonant clusters are allowed as onsets but not codas. For example, /skw/ is licit as an onset (e.g., squirrel), but not as a coda. Similarly, within a language, there are restrictions on the way in which morphemes can combine to form phrases and how these phrases are combined to form clauses. For example, in Chomsky's (1986) Principles-and-Parameters theory, this restriction is cashed out by saying that the ordering of specifier and head and head and complement must be the same for all phrases in a given language.

3.11 Unanswered questions about the genetic studies of language. To the best of our knowledge, no studies have investigated how genetic factors affect aspects of language such as discourse-pragmatic⁸, derivational morphology, or suprasegmental phonology, nor have studies investigated the genetic overlap of linguistic abilities and nonlinguistic abilities such as Theory of Mind, mathematical ability, face recognition, mental representation, etc.. In addition, we know of only a handful of studies that include multivariate analyses of more than two variables, and no studies that simultaneously investigate the genetic overlap among phonologic, syntactic and lexical abilities. Nor do we know of studies that simultaneously investigate overlap among more than one aspect of language and any of the motor abilities included in the PEGI study. Without such studies, one cannot know how specific the genetic factors that affect language (or subcomponents of language) really are.⁹

4. Evolution of language

4.1 Theories about the evolution of language. The intent of this section is not to espouse a particular theory about the evolution of language. Rather, we will attempt to compare some of recent theories about the evolution of language, many of which are described more fully in this volume. Broadly speaking theories about the evolution of language can be characterized along 3 dimensions.¹⁰ The first dimension is the process by which the genetic factors that currently subserve language came into existence. Some theorists (e.g., Pinker, 1994; Pinker & Bloom, 1990) argue that the genetic factors involved in language conferred a reproductive advantage on those who possessed them and therefore these factors were selected for (i.e., natural selection theories, the right side of Figure 1). Other theorists (e.g., Chomsky, 1987; Piattelli-Palmarini, 1989) argue that the evolution of language was serendipitous, with the genetic factors involved in language being passed on to subsequent generations because they happened to be near genetic factors for other functions that were advantageous (i.e. hitch-hiking theories, the left side of

⁸ We have begun to investigate the discourse-pragmatic abilities of the PEGI twins. We are also obtaining measures of the types of social behaviors often seen in children with autism spectrum disorders. In addition to determining the extent to which genetic factors affect these abilities, our goal is to assess the genetic overlap between these abilities and other linguistic and nonlinguistic abilities.

⁹ Currently, we have too few twins in the PEGI study to perform multivariate analyses involving 3 and 4 variables. Our long-term goal is to have enough twins to perform such analyses.

¹⁰ I am indebted to Jennifer Ganger for her insights about the similarities and differences among evolutionary theories of language. An earlier characterization of evolutionary theories along two dimension appears in Ganger and Stromswold (1998).

Figure 1). A second dimension along which evolutionary theories differ is whether *any* of the genetic factors that evolved (via whatever process) were specifically linguistic (language-specific theories, represented by *A* and *B* in Figure 1) or whether all of the genetic factors also subserved some nonlinguistic function (precursor theories, represented by lower case *a* and *b* in Figure 1). The third dimension concerns what functions the genetic factors involved in language support. For language-specific theorists, the question is how specific are the linguistically-specific genetic factors? For example, do these genetic factors only affect some subcomponent(s) of language (e.g., syntax, Bickerton, 1990; Newmeyer, 1991), or do they support specific functions that may or may not be used in more than one subcomponent of language (e.g., recursion, see Hauser et al., 2002). In other words, what is the function of the genetic factors represented by *A* and *B* in Figure 1? For precursor theorists, the question is what nonverbal abilities were co-opted or underlie (some aspects or subcomponents of) linguistic abilities? Among the abilities that have been proposed are oral motor skill (e.g., Lieberman, 1984), fine motor skill (e.g., object manipulation, tool creation or use, Bickerton, 1990; Greenfield & Savage-Rumbaugh, 1990; Greenfield, 1991; Tobias, 1994), nonverbal cognitive abilities (e.g., abstract mental representations such as those needed to think about things, actions or events that are not present in the immediate environment, Gardenfors, 2003), social cognition (Knight, 1998; Worden, 1998), theory of mind (Dunbar, 1998), and mind reading (Origgi & Sperber, 2000).

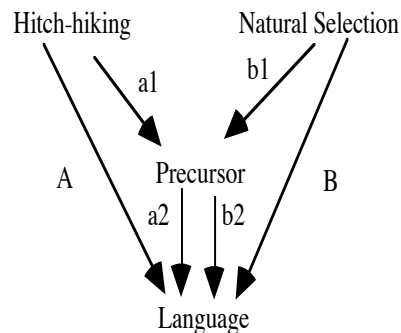


Figure 1: A Schema for Theories of Language Evolution

4.2 Evolutionary implications of genetic findings. The finding that genetic factors play a substantial role in all aspects of language indicates that people differ in their linguistic abilities, and that part of this variance is due to genetic factors and, hence, evolutionary processes could have been involved in all aspects of language. The finding that genetic factors play a smaller role in lexical abilities than syntactic or phonological abilities suggests that environmental factors affect children's lexical abilities more than they do their syntactic or phonological abilities. If genetic factors play a greater role for syntax and phonology, this could indicate that syntax and phonology evolved together and somewhat separately from the lexicon. This could reflect that having a large vocabulary conferred less of an advantage than being syntactically or phonologically gifted or that syntax and phonology both hitch-hiked on another ability that conferred reproductive success.

Behavior genetic studies consistently find that genetic factors play a greater role for the linguistic abilities of language-impaired children compared to normal children. This suggests

that normal and language-impaired children's language may involve different genetic processes. If this is true, it could reflect that somewhat different neural circuitry subserves language in language-impaired and normal children, which in turn would mean that, with respect to language, the evolutionary history of language-impaired and normal children could differ.

If the high degree of genetic overlap for linguistic and oral motor abilities and for linguistic and fine motor abilities reflects shared neural circuitry for abilities that require complex motor control, this could mean that from an evolutionary standpoint, linguistic oral motor abilities are parasitic or coevolved with fine motor and oral motor abilities. Thus, the genetic overlap for linguistic and oral motor abilities supports theories that argue that language evolved from non-linguistic oral motor abilities (e.g., Lieberman, 1984; Locke, 1998; Ujhelyi, 1998). Similarly, the finding that some of the same genetic factors affect linguistic and fine motor abilities is consistent with theories that argue that fine motor abilities were a precursor to language (e.g., Bickerton, 1990; Greenfield & Savage-Rumbaugh, 1990; Greenfield, 1991; Tobias, 1994),

If the genetic overlap for linguistic and social ability indicates that the neural underpinning for social cognition and language are partially shared, this means language could have (partially) evolved from social abilities, consistent with the theories of Knight (1998), Worden (1998), Dunbar (1998), Origg and Sperber (2000) and others. The greater genetic overlap for syntax and phonology than for either the lexicon and syntax or the lexicon and phonology suggests that the evolutionary history of syntax and phonology may be more similar than that of the lexicon and either syntax or phonology. For example, it is possible that genetic factors coded for some function that allowed for the simultaneous development of phonology and syntax.

In summary, results of genetic studies of language are most consistent with linguistic models and evolutionary theories of language that invoke both general and language-specific factors. Unfortunately, although genetic studies of language provide insight about what linguistic and nonlinguistic abilities co-evolved and, perhaps, insight about which abilities were precursors to language, they cannot tell us the process by which language evolved (i.e., natural selection vs. hitch-hiking or happenstance).

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