Theoretical Concepts in the Genetics of Expertise

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What does it mean for a behavioral tendency or skill to be heritable? This basic question is perhaps one of the most vexing and debated issues in all of the social sciences (for a thoughtful discussion of this topic, see Turkheimer, 1998). To many scientists and laypersons alike, the concept of heritability is haunted by the specter of determination and immutability, specifically, that the more heritable a phenotype is, the less experience matters. However, the fallacy of this logic becomes clears when one considers the realm of expertise. Levels of expertise in a wide variety of specialized domains, ranging from playing a musical instrument to performing quantum physics, necessarily rely on the (typically effortful) acquisition of both declarative and procedural knowledge that can only occur through experience. At the same time, a growing body of behavioral genetic research reports moderate genetic effects on interindividual variation in empirical indices of expert skill (Hambrick, Macnamara, Campitelli, Ullen, & Mosing, 2016).

Given that experience is necessary for the acquisition of expertise and that expertise in a wide range of domains is heritable, the intuition that genetic effects compete with experiential effects is clearly flawed. How can genetic and experiential influences on expertise be reconciled? Contemporary work in behavioral genetics (e.g., Moffit, 2005) has come to use the term *gene-environment interplay* as an umbrella term to refer to several dynamic processes through which genetic and experiential factors work together to influence development. In this chapter, I describe how such dynamic processes may be relevant to understanding the development of expertise and to making sense of heritable variation in behavioral phenotypes more generally. I begin by describing what, statistically, heritability refers to.

Heritability: Estimation and Interpretation

Genetic material (DNA) contains the code for creating proteins that are critical to the functions of cells and the tissues and organs that they compose. (DNA also contains sequences that do not code for proteins, but may serve other functions, such as regulation of when and how other segments of DNA are read and turned into proteins.) An overwhelming proportion of the code contained in the DNA of an individual is exactly the same as that of all other humans in the world. It is this commonality that serves as the basis for the physiological and psychological phenotypes that we as a species have in common (e.g., having 10 fingers, 10 toes, and the capacity for language). However, a small proportion of the code in DNA varies from person to

person. The heritability of a characteristic refers to the extent to which this within-species *variation* in genetic code (DNA sequence variation) is statistically associated with *variation* in that phenotype. As it is exclusively an index of association between DNA variation and phenotypic variation, heritability itself is not directly concerned with the genetic basis (or lack thereof) for human universals.

Classical methods in behavioral genetics, such as twin and extended-family studies capitalize on the fact that interindividual differences in DNA sequence variation are not entirely random. Mendel's laws of inheritance (Mendel, 1865) dictate that individuals who are more closely related, in the familial sense, are more genetically similar. (Whether individuals are more similar on a phenotype under study is an empirical question on which the phenotype's heritability estimate is based; see below.) Monozygotic (MZ) twins are nearly perfectly genetically similar; dizygotic (DZ) twins and full siblings share, on average, about half of the genes that vary within the general population; first cousins share, on average, about 12.5% of these genes, and so on. The magnitude of genetic influence on a phenotype (e.g., musical expertise) is inferred from the extent to which, holding amount of shared rearing constant[1], individuals who are more genetically similar (e.g. MZ twins compared to DZ twins) are also more similar on that characteristic. Other sources of variation are also often estimated. For instance, a shared environmental effect on a characteristic refers to the extent to which individuals raised together (e.g., siblings) resemble one another on that characteristic to a greater extent than can be attributed to their genetic similarity alone. For instance, the extent to which similar-aged, biologically unrelated, adoptive siblings tend to resemble one another on the characteristic under study can be taken as an index of the shared environmental effect on that characteristic, because adoptive siblings share a common rearing environment but are expected to be no more genetically similar, on average, than they are to individuals chosen at random out of the population). A nonshared environmental influence refers to the extent to which individuals

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[1] I return to the question of whether more genetically similar people experience more similar environments below. As has been discussed in further detail elsewhere, behavioral genetic methods rely on the "equal environments" assumption that the average range of experiences to which more genetically similar individuals (e.g. MZ twins) have access is no more similar than that for less genetically similar individual (e.g. DZ twins). As a result of more similar preferences, motivations, and aptitudes, more genetically similar individual may seek out and evoke more similar experiences from that range over time. This increased similarity of experience among more genetically related similar individuals is not a violation of the equal environments assumption, but potentially a central mechanism of the translation of genetic variation into phenotypic variation. I discuss such processes of genotype-environment correlation in further detail below.

nearly perfectly matched on their genes and their shared upbringing (i.e., identical twins reared together) are still not perfectly concordant on that characteristic. The nonshared environment may reflect measurement error, as well as environmental effects uniquely experienced by individuals reared together (e.g., different friend groups, difference perceptions of the same event).

Newer methods use measured DNA from unrelated individuals to estimate the magnitude of genetic effects on a phenotype. For instance, recently developed methods (e.g., Yang et al., 2011; also see Bulik-Sullivan et al., 2015) estimate the magnitude of genetic influence on a characteristic from the extent to which unrelated individuals who are slightly more genetically similar also tend to be more similar on that characteristic. Progress has been made in identifying some of the specific genetic variants that account for heritable variation in complex behavioral traits and psychiatric disorders, but it has become clear that many different variants distributed widely across the genome are together responsible for the majority of genetic variation in such traits (Visscher et al., 2012). In other words, it is not the case that only a handful of genetic variants account for the totality of genetic variation in complex behavioral phenotypes.

Regardless of the method used to estimate heritability or individual effects of specific genetic variants, genetic effects by themselves are nothing more than statistical associations, i.e., regression effects. For instance, the heritability of a characteristic can be directly interpreted as the proportion of variance (R^2) in that characteristic when it is entered as the dependent variable in a regression equation in which the independent variable is genetic variation. This is, in fact, exactly how structural equation models that estimate heritability are specified, with one caveat being that the independent variable (genetic variation) is a latent variable that is not directly measured, but inferred from cross-relative covariance information on the characteristic under study. Similarly, genetic associations involving specific DNA measures, whether these be in the context of a *polygenic score* formed as a weighted composite from many different variants or in the context of a score on a single genetic variant (e.g., a single nucleotide polymorphism, or SNP), are also nothing more than regression associations with genes as the predictor variables and the characteristic of interest as the outcome. (Control variables are also typically included to remove confounds between sociocultural stratification and DNA variation associated with racial/ethnic ancestry; Hamer, 2000.)

Because genetic associations are simply squared correlations (i.e., R^2), maxims regarding the ambiguity of correlation and causation apply. As is the case in any observational study, once a correlate of an outcome is detected, much work remains to identify the potentially circuitous pathways of causation, including determining direction(s) of causation, and mediating and moderating mechanisms. Indeed, contemporary research in gene-environment interplay focuses on how environmental experiences moderate the effects of genotype (or, alternatively put, how genotypes moderate the effects of environment) on the development of psychological outcomes and how environmental experiences relevant for this development come to be correlated with genotypes over time. In the following section I discuss how such processes may apply to the developmental of expert skill.

Classical Concepts of Reaction Range

Relative to all other realms of psychological function, it is perhaps most clear that the development of expert skill results from learning through experience. The scientific study of learning is foundational to field of psychology, at least dating back to Ebbinghaus's (1885) work on memory retention and forgetting. Ebbinghaus introduced mathematical functions relating the strength of memory retention to the amount of repetition and retention interval. Importantly, these are some of the same factors commonly examined in modern studies of associations between practice and expert skill acquisition, with intensity of practice constituting a third major factor (Ericsson, 2004; Ullen, Hambrick, & Mosing, 2015). One simplified representation of the relationship between amount of practice and skill level is depicted in **Figure 1**, in which the skill increases with amount of practice, albeit at a decreasing rate.
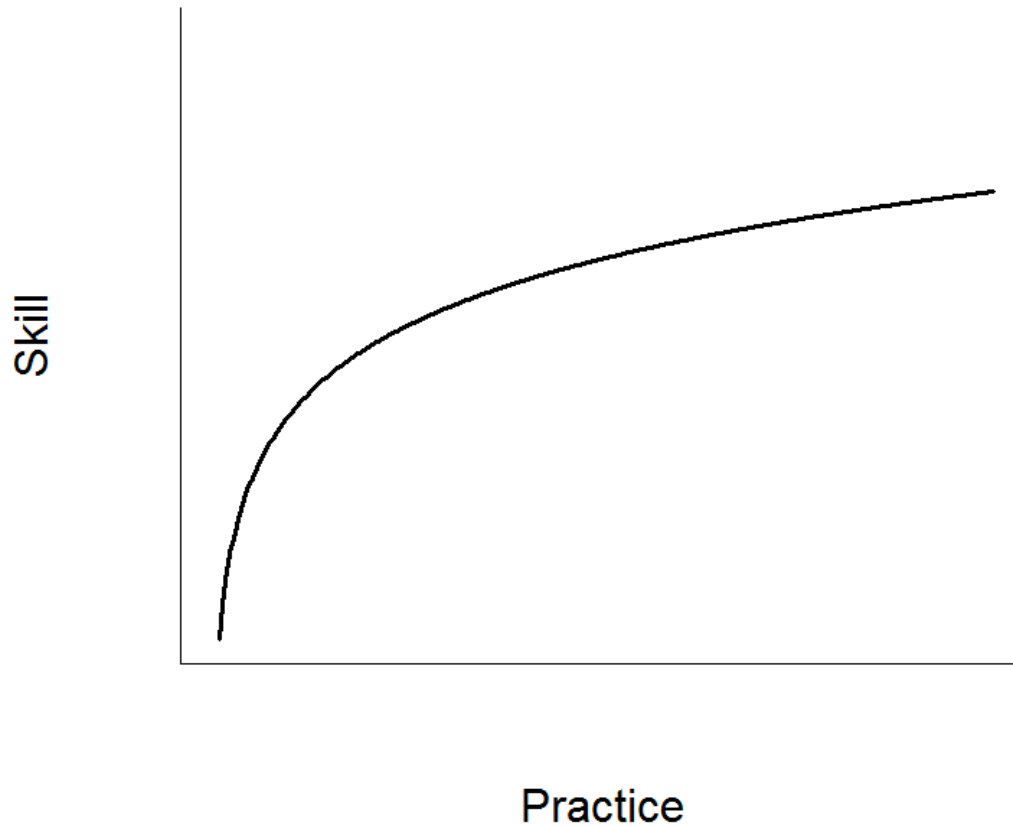
Figure 1. A stylized example a hypothetical learning curve relating skilled performance to amount of practice.

One straightforward conceptualization of the role of genetics in learning is that genetic variation is related to the *slope* of the practice-skill function. This is represented in **Figure 2**, which closely resembles the reaction ranges originally depicted by Gottesman in 1963, based on earlier work from the early 1900s. Gottesman (also see Turkheimer & Gottesman, 1991 and Gottlieb, 1997) hypothesized that the function relating the level of the phenotype to environmental quality (e.g. amount or quality of training or practice) might differ according to genotype, such that genotypes differed in the range (distribution) of probable levels on the phenotype (e.g., skill) under study. Under this framework, the genotype-specific ranges of skill

often overlap, and where within the genotype-specific range a skill level is manifest depends on the quality of the environment, or in this case, the amount of practice. Moreover, the reaction range only applies to the range of environmental experience (practice) observed in the empirical data. While extrapolation to unobserved ranges of quality or amount of environmental experience is possible, there are not guarantees that such extrapolation may be accurate.
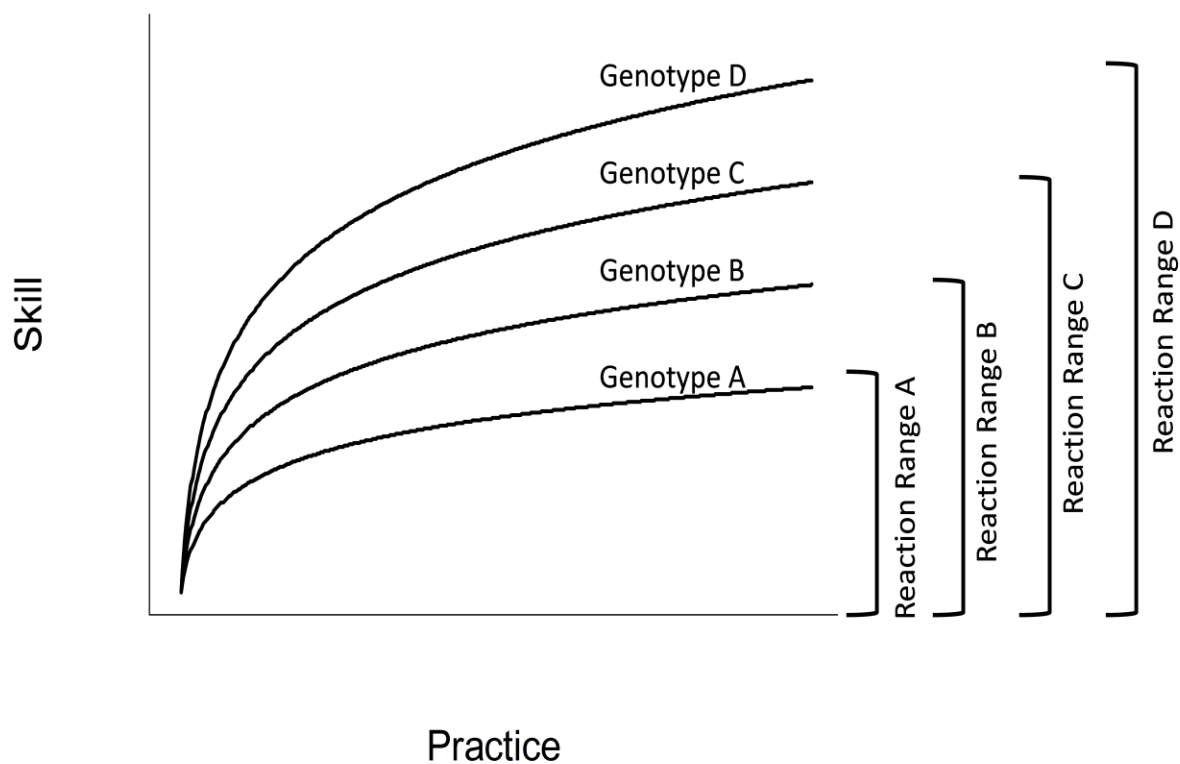
Figure 2. A stylized adaptation of Gottesman's (1963) concept of reaction range to the development of skilled performance with practice.

We can extend the stylized learning curve presented in Figures 1 and 2 by situating the accrual of practice within time, thereby allowing for time intervals between repetitions (e.g., practice sessions). As originally described by Ebbinghaus (1985) and depicted in **Figure 3**, some degree of loss may occur during these intervals. This stepwise, or sawtooth, pattern of skill development resembles patterns that feature prominently in contemporary developmental models

of skill development (e.g., Seigler, 1999), as well as classical Piagetian concepts of assimilation of accommodation (Piaget, 1952).
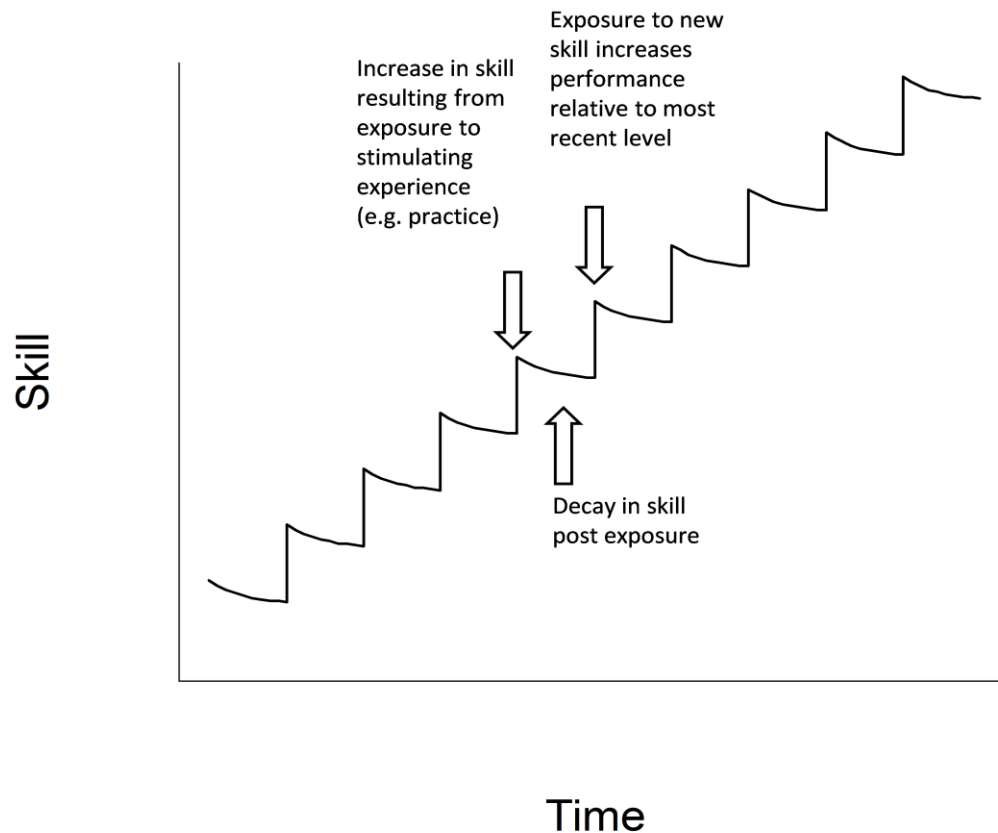
Figure 3. A stylized hypothetical example of learning response to discrete practice sessions separated in time, and forgetting during the inter-practice interval.

Extending this pattern to allow the benefit of each individual experience (practice session) to be differential by genotype creates a pattern of differential accrual of skill over time, illustrated in **Figure 4.** In this example, genotypes engage in equal frequency of practice and differ in in the benefit of each practice session. This pattern of initial differences magnifying over time, such that "the rich get richer," has been referred to as a *Matthew Effect* (Stanovich, 1986).
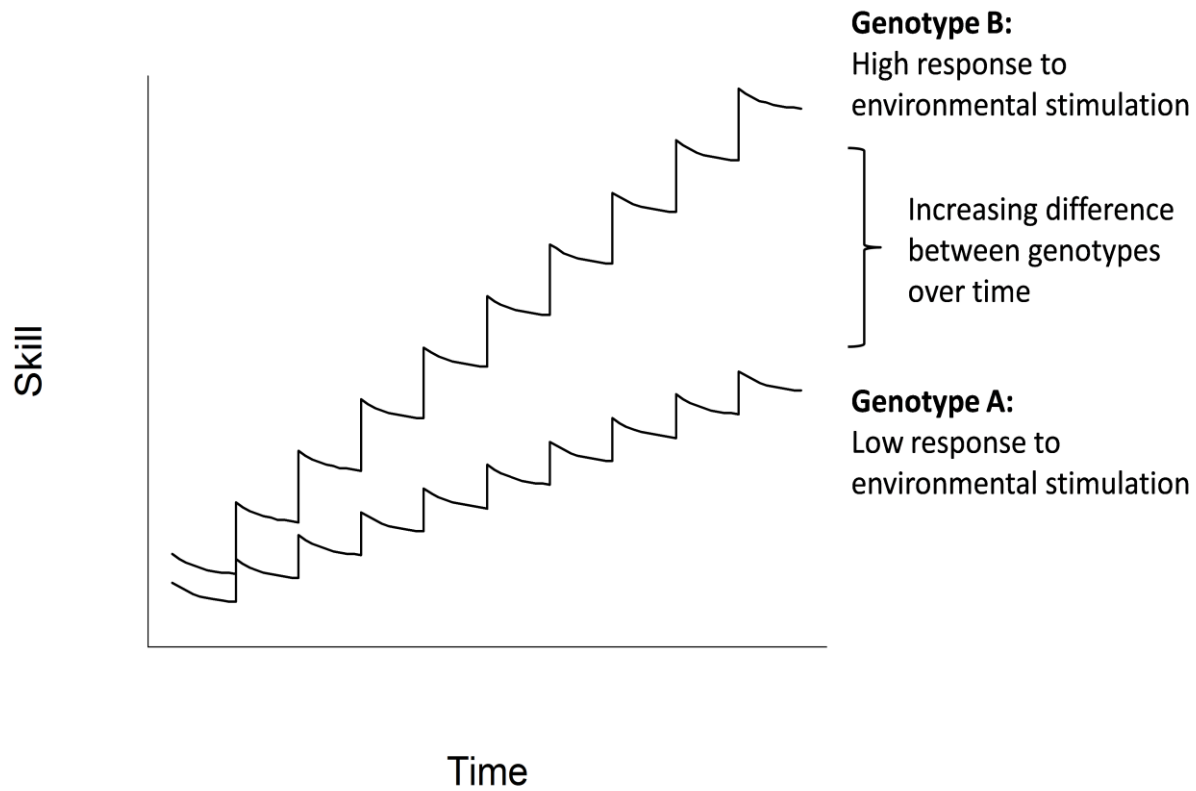
Figure 4. A stylized hypothetical example of genetic differences in learning response to discrete practice sessions separated in time. Both genotypes are exposed to the same schedule of practice.

Developmental Concepts of Gene-Environment Transaction

In controlled experiments on learning, the schedule of training and practice is determined by the researcher, and differences between individuals in the pace of learning can be cleanly separated into components associated with manipulations of the training regime (typically the active training condition vs. no-training control), those associated with naturally-occurring (oftentimes pre-existing) individual differences in skill, and those associated with individual differences in response to the training or intervention (Tucker-Drob, 2011). However, outside of the laboratory, where most expert skill acquisition actually occurs, the amount, frequency, and intensity of training and practice are nonrandomly experienced by individuals. From a classical experimental perspective, such selection effects are inconveniences that muddle the strength of

causal inferences that can be made from observational research. However, selection effects may not simply be methodological nuisances, but rather key mechanisms of the differentiation of expert skill by genotype "in the wild."

Plomin, DeFries, and Loehlin (1977) described a conceptual taxonomy of genotype-environment correlation, the tendency for exposure to environmental experience to differ by genotype. Passive gene-environment correlation refers to situations in which offspring inherit genes from their biological parents that also influence those parents to provide the rearing environment that they do. For instance, a parent who has passion for and skill at playing musical instruments may both raise his or her child in an environment that is particularly conducive to fostering the development of musical expertise, and also pass on that child a genetic dispositions for passion and talent for music. Active gene-environment correlations refer to situations in which individuals seek out certain environmental experiences on the basis of their genetically influenced characteristics. For instance, children genetically disposed toward a passion for music may actively pursue musical training. Evocative gene-environment correlation refers to situations in which individuals evoke environmental experiences based on genetically-influenced traits from the people and institutions around them. For instance, children who show an early aptitude for playing a musical instrument in the context of a music course that is offered to all students might by encouraged by classmates or selected by teachers to join extracurricular musical training, join a band, or enroll in specialized music coursework.

Active and evocative genotype-environment correlations may serve as the basis for dynamic feedback processes in which individuals differentially select and evoke differences in environmental experiences, such as practice, on the basis of their genetically-influenced characteristics, and these experiences in turn affect the development of expert skill, while at the same time reinforcing the original characteristics that drove the selection and evocation. Characteristics that lead people to differentially select and evoke environmental experiences such as training and practice have been termed *experience-producing drives* (EPDs; Bouchard, 1997; Hayes, 1962; Johnson, 2013). Experience-producing drives may include interests, proclivities, motivations, goals, and aptitudes for the skills being acquired (Tucker-Drob & Harden, in press). As dynamic processes unfold, experience and the skills that benefit from experience become increasingly differentiated by genotype, again producing a *Matthew Effect* in which the "rich get richer." This is illustrated in **Figure 5**. Importantly, **Figure 5** illustrates a situation in which the
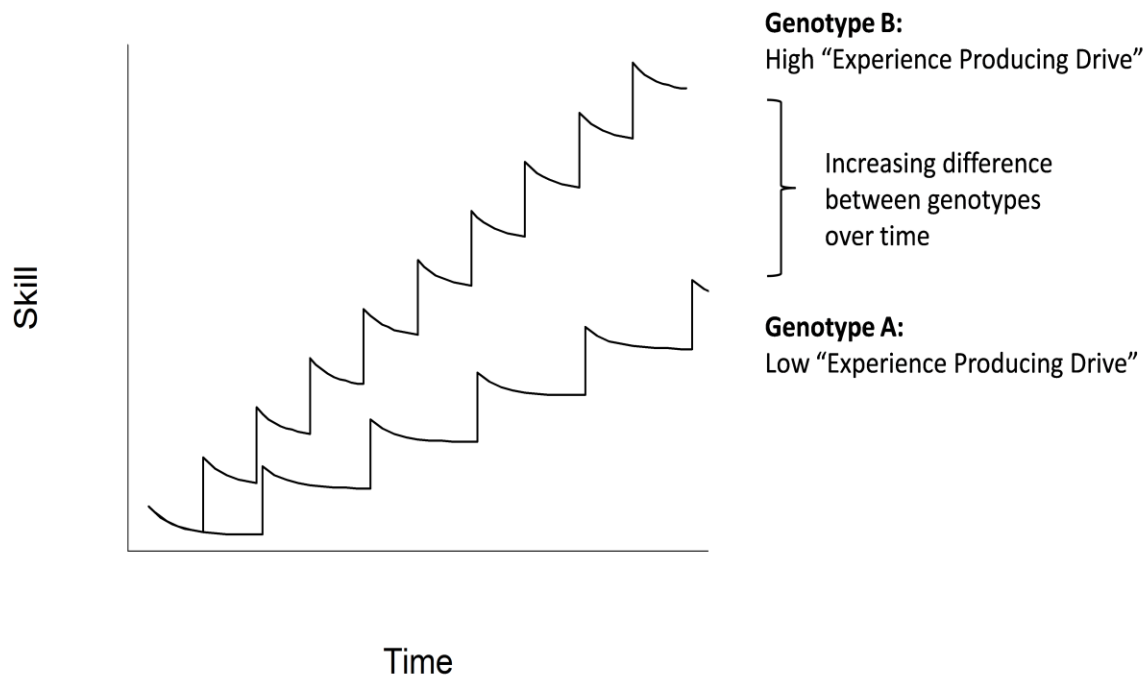
Figure 5. A stylized hypothetical example of genetic differences in drive to engage in discrete practice. Both genotypes respond equivalently to each discrete practice session, but the genotypes differ in the frequency of practice.

increment in skill that is associated with each specific learning experience (practice session) is equivalent across genotype, as is the rate of decay of skill post exposure. The genotypes only differ in their frequency of exposure to the learning experience. In other words, the amount of experience comes to be correlated with genotype, such that environmental experience itself is "heritable" (Plomin, 1994).

Multiple Processes May Simultaneously Differentiate Skill by Genotype

The processes described above have the potential net effect of differentiating skill by genotype over time. **Figure 4** depicts a situation in which genotypes differentially benefit from a given practice or training session, but the frequency of practice and training is held constant

across genotypes. **Figure 5** depicts a situation in which genotypes equally benefit from a given practice or training session, but –as a result in differences in motivational factors- the frequency of practice and training is differential by genotype. These processes may of course co-occur, leading to even more rapid differentiation of skill by genotype over time. Additionally, I have cast the former situation in terms of differences in responsivity to environmental stimulation, which lends itself to conceptualizing the different genotypes as corresponding to different inherent aptitudes. However, the former scenario may also stem from genetically influenced individual differences in motivational factors or experience-producing drives leading to differences in the extent to which individuals effortfully engage with the training material or practice. By the same token, the latter scenario could result from a feedback processes in which individuals who experience training or practice as being particularly difficult or producing minimal results become less motivated to pursue frequent or intensive practice or training. Thus, both genetically influenced aptitudes and experience-producing drives may be play roles in the hypothetical patterns depicted in both Figures 4 and 5.

Growing Differences between Genotypes over Time Imply Increasing Heritability

Thus far, I have characterized genetic effects in terms of differential profiles of skill development by genotype. Importantly, interindividual differences in genetic propensities and aptitudes are unlikely to be distributed into a few discrete categories, but are better described by continuous distributions. I have chosen discrete genotype values for illustrative purposes, in the same way that specific levels of a continuous moderator are chosen for plotting simple slopes in a linear regression with an interaction term. Particularly when one bears in mind that genotypes are continuously distributed, it becomes clear that the patterns of diverging means by genotype that are depicted in Figures 2, 4, and 5, imply increasing heritability of skill over time. As described earlier, heritability refers to the amount of variation in a phenotype (e.g. skill) statistically accounted for by genetic variation, expressed as a proportion of total variation in the phenotype. For instance, in Figure 2, it can be seen that mean skill levels for each genotype become increasingly separated as practice accrues, such that genetic differences statistically account for increasing amounts of variation in skill with the accrual of practice. Unless environmental variation unique of the practice itself also explains an increasing amount of variation in skill as practice accrues (such that the relative proportion of genetic variation to total

variance remains constant or decreases), the patterns depicted in Figures 2, 4, and 5 directly imply that heritability will increase with the accrual of practice. Indeed, in the area of cognitive ability (which one might consider a form of expertise), there is strong evidence for increasing heritability over child development (Tucker-Drob, Briley, & Harden, 2013; Briley & Tucker-Drob, 2013). In the realm of motor learning, Fox and colleagues (1996) reported genetic influences on rate of learning for a rotary pursuit task that resulted in increasing heritability on task performance over the course of practice. More recently, Hambrick and I (Hambrick & Tucker-Drob, 2014) reported evidence of higher heritability of music accomplishment (e.g., performing with a professional orchestra, receiving a high rating in a musical contest) among adolescents who reported regularly practicing a musical instrument, compared to those who reported not practicing. Other patterns are, of course, possible. For instance, if mean skill levels for different genotypes converge after prolonged practice, the implication would be decreasing heritability over time. Ackerman (2007) for instance, proposes that whether a task is *open* (such that there is no upper limit to the skill level that can be attained with further practice or training) or *closed* (such that there is a finite upper level of skill that can be attained) is the major determinant of whether interindividual differences in skill levels will converge or diverge over time.

The "Cafeteria" of Experience and Gene × Environment Interaction

The "cafeteria of experience" (Lykken, Bouchard, McGue, & Tellegan, 1993) refers to the assorted variety of possible experiences to which individuals have access, just as in a dining hall cafeteria where an assortment of food options are available from which to choose. Each individual may choose a different set of experiences (or food items) from the cafeteria, but in a given cafeteria, the same experiences (or food items) are available to everyone.

Scarr & McCartney (1983) proposed that, as infants develop into children, children into adolescents, and adolescents into adults, increasing autonomy to select and evoke environments within their surrounds may lead to further differentiation of experience and skill by genotype. Keeping with the cafeteria analogy, we would anticipate that the diversity of experiences from which to choose increases over child development. However, not all individuals have access to the same cafeteria or variety of experiences from which to choose. For instance, some children are never given the opportunity to take piano lessons, or even place their fingers on a piano. In

such a case, no matter what an individual's drive, desire, or aptitude for learning piano may be, it is highly unlikely that she or he will be able to engage in piano training or to practice to the extent necessary to become an expert pianist. Thus, one would expect that genetic influences on skilled performance would be most expressed in contexts of high access to the experiences and resources necessary for accruing expertise in the domain under study (Scarr, 1992; Briley & Tucker-Drob, 2015). Indeed there is some evidence that such a pattern applies to the heritability of cognitive ability as a function of socioeconomic opportunity (Tucker-Drob & Harden, 2012; Tucker-Drob & Bates, 2016). Importantly, the availability of experiences and resources does not guarantee that expertise will be attained (genetically-influenced drives and aptitudes are likely to be the other key ingredients), but without a sufficient cafeteria of experience, attaining expert skill levels is predicted to be exceedingly unlikely.

Conclusions

In this chapter I have provided a conceptual framework for research into genetic effects on expert skill; this framework explicitly relies on empirical and logical truths regarding the role of environmental experience on skill development. I have proposed the genetic variation may relate to skill development both in its relationship to heterogeneity in the effect of training and practice on skill development, and in its relationship to experience-producing drives that lead people to differentially engage in frequent effortful training and practice necessary for skill development. Further, I have proposed that both expert levels of practice and genetic effects on variation in expert skill level depend on the availability of a cafeteria of experience that includes access to opportunities for training and practice related to the skill under investigation.

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