The London School of Economics and Political Science

Cultural evolutionary production of human psychobiological variation and function

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Declaration

I certify that the thesis I have presented for examination for the MPhil/PhD degree of the London School of Economics and Political Science is solely my own work other than where I have clearly indicated that it is the work of others (in which case the extent of any work carried out jointly by me and any other person is clearly identified in it).

I declare that my thesis consists of 70137 words (from Chapter 1 to Chapter 7 inclusive)

Statement of co-authored work

I confirm that Chapter 3 was jointly co-authored with Dr. Michael Muthukrishna and Dr. Rachel Spicer. I contributed 80% of this work.

I confirm that Chapter 4 was jointly co-authored with Dr. Michael Muthukrishna. I contributed 90% of this work.

I confirm that Chapter 6 was jointly co-authored with Dr. Michael Muthukrishna. I contributed 90% of this work.

Abstract

This thesis presents a framework for understanding how the organisation of the human mind and its psychobiological basis are produced through the mechanisms of cultural evolution. It foregrounds three characteristics of the human mind: its cross-cultural variation, its responsiveness to environmental inputs, and its collective construction. Each of these characteristics has been studied on its own, but cultural evolution serves as an integrative theoretical framework for understanding how they relate to each other. A key insight is how the developmental environment is shaped extensively by cumulative cultural evolution, allowing culture and nervous system to be meshed in a functionally productive and highly evolvable coupling. Classical conceptions of nature and nurture are insufficient for capturing this dynamic, and instead reinforce conceptual and methodological barriers that obscure the effect of culture. This thesis articulates a theoretical interface that allows a number of insights derived from cultural evolutionary theory to be productively employed within the psychological sciences—fields such as psychology, behavioural biology, behavioural genetics, developmental science, and cognitive neuroscience.

Chapter 1 briefly introduces the subsequent chapters, and Chapter 2 charts the overall theoretical framework of the thesis. Chapter 3 attempts a theoretical integration of cultural evolution and behavioural genetics in particular, offering new insights about the interpretation of genetic effects like heritability. Chapter 4 is an empirical test of a prediction given in the prior chapter, and demonstrates how cultural variance influences heritability across countries. Chapter 5 shows cross-cultural variation in the structure of internal representations using factor analysis and a questionnaire, and provides preliminary evidence that writing systems shape mental organisation. Chapter 6 proposes a theoretical integration between cultural evolution and neuroscience. Taken together, these studies give substance to a novel theoretical framework for the psychological sciences that elucidates the rich coordination of mind, biology, the developmental environment, and cultural dynamics.

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I would like to thank my father, my mother, and my sister for remaining unconventionally calm even after learning about my Big Plan to move from suburban Tokyo to rural Canada at age 27 to pursue an undergraduate degree in psychology—with the distant goal of completing a PhD. I now find myself at the endpoint, which used to be far beyond the

horizon; I'm grateful that each of you were there by my side from the point of departure, calmly looking forward with me into the hazy distance.

Along the way I also met my wife. I would like to thank Yimin, who has transformed my life with her radiant heart. It is a joy to be weaving our journey.

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Chapter 1: Introduction to the thesis

This thesis explains how the organisation of the human mind and its psychobiological basis are constructed in part by cultural evolution. A general theoretical framework is first given, and buttressed by specific theoretical analyses that extend the general argument to the disciplinary domains of behavioural genetics and cultural neuroscience. Empirical analyses support the framework by confirming a preregistered prediction given in the theoretical analyses of behavioural genetics on the one hand, and by revealing theoretically meaningful cultural variation in the structure of internal representations, on the other. Collectively, these analyses therefore demonstrate how *genes, brains, and thoughts* can be conceptually situated within the overall theoretical framework.

Cultural evolution as a field has its origins in anthropology, and accordingly, has tended to focus on cultural traits such as social norms, tool-making, and food production. I attempt to reconfigure the theoretical apparatus of cultural evolution for use in the psychological sciences, and therefore extend the notion of a cultural trait to psychological and behavioural traits across the board. Various authors have outlined or pursued similar research approaches, but the unique contribution of the present thesis is its elaboration at a psychobiological level of analysis, grappling with topics such as gene–environment interaction and the evolution and development of the brain. This approach, compared to those that revolve around behaviour alone, gives the framework a firm conceptual founding with respect to psychological phenomena, and also offers a richer integration with well-established evolutionary research programmes within the domain of psychobiology.

The present thesis therefore also serves as a prototype for a domain of research that might be appropriately described as *cultural psychobiology*. The term "psychobiology" (as well as the similar term "biopsychology") was formerly a widely adopted label for a whole field of research, but has been out of vogue ever since much of this work was rebranded under the label "behavioural neuroscience", presumably due to semantic prestige. Both psychobiology and behavioural neuroscience refer to the study of the biological basis of mental processes. But implicit in the latter moniker is a theoretical commitment to isolating the nervous system as the biological basis of the mind. There is no doubt that genes are also part of the explanation, but the behavioural neuroscientist, at least in the present caricature, is concerned only about genes expressed as variation in some structure, process, or behavioural output of the brain. He who understands the brain has cracked the mystery of the mind.

My goal in this thesis is to articulate how the biological basis of the human mind is not just the brain or the genome, but a higher-order distributed system that is made up of a community of brains (and the individuals that contain them) that transfers information within- and cross-generationally, systematically guiding the development of other brains in an open-ended manner through the dynamics of cumulative cultural evolution. The aim is a shift in perspective with respect to what is upstream and what is downstream—or rather, whether this sort of linear structure has any meaning—in the production of psychological and behavioural phenotypes. The biological study of this distributed system requires integration across a number of sub-fields of the biological sciences, including neuroscience, behavioural genetics, evolutionary biology, behavioural ecology, and development. Therefore, what is required is not a cultural neurobiology or a cultural genomics, but a more general descriptor—hence cultural psychobiology.

The theme of the present thesis is a culmination of my cross-disciplinary academic background, which has touched upon, to varying degrees, areas of study such as cultural evolution, evolutionary biology, mammalian brain evolution, cognitive neuroscience, cognitive and cultural psychology, self-organising systems, anthropology, and philosophy of mind. In retrospect, I realise that the worldview that informs this thesis has also been influenced by my early training in spatial and architectural design. Every new thing we do emanates from our origins.

Most of the chapters in this thesis have either been published or are somewhere in the publication pipeline. Their current status at the time of submission of this thesis are as follows:

- Chapter 3 is in press as a target article in the journal Behavioral and Brain Sciences. Co-authors are Rachel Spicer and Michael Muthukrishna.

- Chapter 4 is in preparation for submission to a peer-reviewed journal. The format of the chapter follows the submission format for the journal Current Biology. Co-author is Michael Muthukrishna.
- Chapter 5 is in preparation for submission to a peer-reviewed journal.
- Chapter 6 was published in 2021 as Chapter 3 of the *Oxford Handbook of Cultural Neuroscience and Global Mental Health* (Eds. Chiao, J. Y., Li, S., Turner, R., Lee-Tauler, S. Y., & Pringle, B.). Co-author is Michael Muthukrishna.

The writing in this thesis switches between British and American spelling. Some of this mixing is due to journal-specific publication requirements, but some of it is due to the general messiness of habit that comes from my cross-Atlantic training. I apologise (and apologize) for the stylistic disarray.

Chapter 2: Theoretical framework

Nature–nurture seen through a cultural evolutionary lens

Collective construction of the human mind

What role does cultural transmission play in the production[1] of human minds? This is the research question that I will pursue in my dissertation. Answering this question will require a conceptual shift from the individual-based view of the human mind that has pervaded the psychological sciences over its history toward one that focuses more on collective and socially distributed processes that have all along been shaping human mental capacities.

Although there are myriad ways in which psychologists talk about minds, one common attribute that stands out is what we might call *entitativity*: minds are fundamentally linked to individual persons and reflect the goings-on of their internal lives. This baseline psychological view may be based on the properties of folk psychology (Frith & Frith, 2012; Waytz et al., 2010) working its way into the academic domain, or it may be rooted in Western traditions of thought that continue to resonate in the discipline of psychology today (e.g., Descartes, 1641/1993). Alternatively, it may be the consequence of more recent tactical decisions within the field, for example to enshrine the individual as the basic theoretical unit of analysis, even when studying their sociality (Allport, 1962). Whatever its origin may be, it is clear that the field of modern psychology revolves around this framework of the mental individual, and it has indeed been wildly successful: we know considerably more about everything ranging from attention and memory to emotion and moral judgment than we did several decades ago, as an outcome of this research approach.

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[1] I use the term "production" here instead of "development" to circumvent the latter's connotation of a process that unfolds primarily within the individual, where the surroundings only play a supporting role. This may be satisfactory for something like fetal development but is undesirable when characterising a process based on cultural transmission.

Other disciplines such as human evolutionary biology take a rather different approach toward human behaviour. Because evolutionary history is fundamentally grounded in population dynamics, researchers working in this field often look at the *collective* organization and processes that explain genotypic and phenotypic change (e.g., Wilson, 2012a). This approach also serves as the foundation on which evolutionary theory finds bridges with the social sciences, in particular those branches of social science that focus on collective or coordinated behavior, such as parts of economics (Gintis et al., 2008; Nunn, 2020a). From imitation and language to norm adherence and large-scale cooperation, many aspects of human uniqueness cannot be sufficiently explained without a population framework. But such traits are typically also grounded in mental processes that are complex and opaque, and the population approach often coarsely abstracts or diminishes the contribution of these individual psychological processes for the sake of explanatory coherence at the collective level.

Within the psychological sciences, there have been sporadic efforts to extend both theory and empirical investigation into multi-agent situations that exhibit non-trivial interaction between the psychologies of individuals (Fusaroli et al., 2014; Goldstone & Theiner, 2017; Higgins et al., 2021; Hirst et al., 2018; Hutchins, 1995; Raafat et al., 2009; Sebanz et al., 2006). These projects have produced various promising insights but their impact on the field at large has been limited, and they often remain fragmented from each other, presumably due to the difficulty of articulating an overarching theoretical framework. However, given that much of the biology of human behavior appears to depend upon collective-level explanation, we may assume that progress in the science of the human mind will require a reconciliation of the individual-based framework of mind with a collective framework of behavior. A sharp division of labor between the study of collectives and individuals is not a promising strategy going forward into the future—it is unrealistic to expect that the true nature of the evolutionary origins, development, and informational architecture of human minds will be uncovered without eventual convergence in the pursuit of the individual and the collective. The psychological sciences are still a young discipline in relation to the timescale of scientific progress, and the situation may be analogous to other episodes of unification between levels of analysis in the history of science: for example between gas laws and molecular dynamics in thermodynamics or between trait heredity and ecological diversity in evolutionary biology.

The collective processes that I focus on in my dissertation are those that have found expression within cultural evolutionary theory (e.g., Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Henrich, 2016). This is a framework that explains how humans use social learning (e.g., selective imitation or conformist learning) in a strategic manner to acquire adaptive behaviours without paying the cost of discovering them anew through individual learning (e.g., trial-and-error). Here, culture refers to the accumulated body of behavioural and psychological traits that can be transmitted among individuals both within and across generations. Social learning has been given a substantial amount of treatment within psychology (Asch, 1956; Bandura, 1977a; Gergely et al., 2002a), but it has for the most part been studied as one out of a multitude of psychological processes, in which there is no obvious reason to focus on it more than, say, working memory or empathy or proprioception. Within the cultural evolutionary framework, social learning plays a fundamental role in the explanation of human evolution as well as various aspects of contemporary human behaviour, and is the key to explaining our conspicuous behavioural divergence from chimpanzees since the last common ancestor (Herrmann et al., 2007b; Whiten et al., 2009a).

Whereas psychology focuses on how information-processing occurs within the mind of an individual, and occasionally among individuals, cultural evolution discusses how information-processing occurs at the level of populations. Cultural evolution is an example of *collective intelligence* (Couzin, 2009; Goldstone & Theiner, 2017; Malone et al., 2010), which is a concept that refers to the processes by which complex, adaptive outcomes are realized at the group-level by emerging from relatively simple processes at the individual-level. An example of collective intelligence from the non-human animal world is how a honey bee swarm can search for candidate nest sites using a socially distributed decision-making process whose aggregate effectiveness far outstrips the ability of any individual bee (Seeley & Buhrman, 1999).

In the case of these bees, the collective outcome is a reliable transition to a new nest site. In the case of cultural evolution, the collective outcome is the construction of new psychological and behavioral phenotypes. There may also be other outcomes such as an increase in the size of groups without a breakdown in cooperation (Henrich & Muthukrishna, 2021; E. O. Wilson, 2012a), but these outwardly social changes are commonly accompanied by a change in psychology as well, and the causal relationship between these internal and external factors is complex and likely to be interactive rather than a linear progression (Chudek & Henrich, 2011). Therefore, the emergence of new psychological and behavioral phenotypes is not just an epiphenomenal outcome of social change, but can in fact feed back into the mechanics of the collective process, giving cultural evolution an interesting and productive circularity. This circularity between mind and society has likely been a key feature of human evolution, and without it, any understanding of the human mind will be limited at best. An assumption of analytical separability between the collective and individual behaviour is likely to be untenable, and a deeper understanding of human psychology will require us to articulate the role that cultural evolution plays in the construction of human minds.

The breadth and depth of cultural learning

If cultural evolution is fundamental for human psychology in the way that I have described, why have psychologists largely failed to focus on this aspect of their subject matter for so long? One major impediment has been the historically entrenched idea that the most natural way to understand the formation of a human mind is to separate it into an innate, genetic component and an experience-dependent, environmental component, often referred to as nature and nurture. Nature represents the idea that behavioural traits like intelligence, creativity, industriousness, altruism, and empathy already lie dormant within genetically transmitted material even if expressed only later in life. Nurture represents the idea that experiential factors such as parenting, schooling, and socioeconomic deprivation or affluence are able to shape behavioural traits. Nature–nurture has been a critical axis of discussion throughout the history of the psychological and behavioural sciences, with schools of thought including phrenology, psychoanalysis, structuralism, behaviorism, classical cognitivism, connectionism, and evolutionary psychology each staking its own position on the issue. Nature–nurture has also regularly captivated the public imagination, as it impinges upon a range of social issues including educational policy, criminal punishment, wealth redistribution, child-rearing, and immigration (e.g., acculturation). The nature–nurture discussion is compelling due to its far-reaching implications for scholars and laypeople alike.

The conventional nature–nurture framework casts learning as a passive process, with the receptive child being provisioned with a rich menu of carefully tuned inputs such as praise, punishment, manners, moral principles, spiritual beliefs, work ethic, heritage, vocabulary, rhetoric, and mental skills, as well as more material inputs such as physical comfort, nutrition, and medical care. These are also the kinds of things that parents typically worry about while raising their children. I will call this general view “folk-nurture”. In contrast, the cultural evolutionary framework postulates that each learner is faced with the fundamental problem of choosing what to learn, an active process. The premise here is that there is often a range of variants to choose from when learning a skill or an attitude or a piece of knowledge, and learners are motivated to pick the most effective variant as efficiently as possible. Ways to achieve this include learning from successful individuals (e.g., star athletes), learning from individuals who are similar to oneself (e.g., from the same social class or ethnic group), or learning from the majority (i.e., conformity). These are all examples of *social learning strategies* (Kendal et al., 2018; Rendell et al., 2011a). Typically, the more complex a society is, the more cultural variants there will be available (due to factors like population size and division of labor), and the more important effective social learning strategies become for sorting through the variety. In such complex conditions, social learning is anything but passive exposure.

Rather than being like a fixed pipeline through which folk-nurture can be deliberately pushed through by caretakers, the learning process is more like a noisy search across the whole society. Learning comes from a wide range of sources, not just parents, teachers, and other guardians: the tendrils of learning are far more wild, prolific, and far-reaching than classical ideas of nature–nurture would have it. The ability to access distant models is considered significant in the cultural evolutionary framework (as well as in social network analysis, see Granovetter, 1973; Watts & Strogatz, 1998), and human behavioural learning is indeed influenced even by the most distant, hard-to-access members of a society (e.g., celebrities). The default assumption of folk-nurture—or provisioning of input by frequently encountered kin and other close associates—is thus unrepresentative of the actual interface that connects learners to environments, and it fails to take into account how the interface is actively shaped by the learner.

Compared to the cultural evolutionary model of learning, the conventional nature–nurture model is truncated along multiple dimensions. It is first of all truncated along the temporal or diachronic dimension. On the standard psychological view, learning occurs, a phenotypic outcome is realised, and that is the full extent of the process of learning. In real societies, a phenotypic outcome in fact serves as potential material to be learned by future generations, which is the basis for *cumulative cultural evolution*: the accumulation of culturally transmissible knowledge over repeated generational cycles of cultural learning (Dean et al., 2014a; Henrich, 2004a; Mesoudi & Thornton, 2018; Tennie et al., 2009a). Although some cumulative culture is found in non-human species (Whiten, 2019), for humans it is a principal feature of our behavioral phenotype, and is a prerequisite for explaining why only we as a species have things like advanced tools, institutionalized social norms, and scientific knowledge. Due to this process of environmental build-up over many generations, the range of available environmental variation is determined by those environments that were accessed by the previous generation, which are in turn determined by the generation before that one, and so on. In taking the current day environment as a given, rather than something that is constructed through repeated inheritance, we abstract away the cumulative processes that render its existence possible in the first place. This biased starting point is also an example of an *observation selection effect* (Bostrom, 2002), which arises when observed data are correlated with the causal pathways that are necessary for the observer to exist, thereby giving the false impression that the data are naturally “this way”.

The nature–nurture model of learning is also truncated along the contemporaneous or synchronic dimension, because it tends to focus on average learners and average environments, whereas cultural evolution places explicit emphasis on the whole distribution of environmental variation and learning outcomes. Because the learner itself is engaging in a search for an advantageous learning environment, the distribution of environments is what sets the constraints on this active search. This kind of synchronic breadth is what allows innovations that arise in one part of society to spread broadly, but the nature–nurture framework often fails to address it due to its implicit emphasis on vertical transmission (i.e., from parents to offspring), as can be seen in the conventional focus on household influence in behavioral genetics. In human societies, oblique (i.e., from non-parent adults to members of the next generation) and horizontal (i.e., among peers) transmission play a crucial role (Henrich & Henrich, 2010; Hewlett et al., 2011; Kline et al., 2013; Mesoudi, Magid, et al., 2016a; Muthukrishna et al., 2014), but these modes of learning are typically not incorporated into the nature–nurture framework (Harris, 1995a). Truncation along both the diachronic and synchronic dimensions severely restricts the explanatory capacity of this conventional framework.

A related point to synchronic truncation is that the cultural evolutionary perspective on learning has a certain notion of probabilistic environmental structure that is lacking in the nature–nurture model. Everything that one learns through cultural transmission—how to tie a knot, the concept of number, the fact that thoughts cannot influence weather (i.e., causal models)—can hypothetically all be learned through individual discovery as well, but the likelihood that these traits will be acquired through individual learning rapidly diminishes in proportion to their dependence on cumulative cultural evolution. Knot-tying is much more likely to be learned in a society in which people regularly tie knots, and even more likely if there is a tradition of teaching in the society. Modern societies have compulsory schooling with standardised curricula, in which the probability of learning components of the criteria approaches 100% in some cases. This probabilistic character arises from the population structure of learning that is inherent to cultural evolution.

The heritability paradox

Imagine that a heritability study reports that 90% of variation in some phenotypic trait of interest is explained by genetic variation and only 10% by environmental variation. We may be inclined to conclude that this trait is overwhelmingly genetic. But because any extant human environments are already the product of extensive cultural evolution, such numbers often do not mean what they seem to mean. Importantly, cultural transmission modulates phenotypic variation. For example, if parenting styles are copied selectively from successful parents, this will reduce the variation in parenting style within the population. Because cultural transmission constitutes extra-genomic inheritance and is attributed to the environmental component of phenotypic variance, the proportion of the phenotypic outcome explained by genes—and hence heritability—is necessarily increased when cultural influence narrows down the range of models who are copied in this manner (Uchiyama et al., forthcoming; Chapter 3 of this thesis). Conversely, when an innovation is being diffused through a population, phenotypic variance explained by the environment increases, and heritability drops. These are straightforward consequences of the formulation of the heritability statistic, and the role of the genetic component increases or decreases not because something has changed about the genetic basis of the outcome, but rather because cultural evolution is shaping the environment.

Cultural evolution also has the effect of indirectly reducing the effect that exogenous environmental variables—those which are not themselves culturally transmitted—have on the outcome variable. For example, when there is an event like the sudden loss of livelihood, its impact on the phenotypic development of the child will depend upon parenting style (among other things). Some parenting styles, like those that involve a network of secondary caregivers, are more likely to mitigate the deleterious effect. This is an example of culture modifying the selection pressures that act upon a population, otherwise known as *cultural niche construction* (Fogarty & Creanza, 2017; Laland & O'Brien, 2011)—the involvement of secondary caregivers carves out a cultural niche in which loss of livelihood has less effect on the well-being of children. In addition, culture can also mask and unmask genetic variation, such as when nutritional supplements mask deficits in the endogenous synthesis of particular compounds, or when improved nutrition reveals genetic variation in abilities that only emerge in stable environments. In these ways, culture can modulate the contribution of the environment to phenotypic outcomes, ensuring that indices of genetic effects (and equivalently, indices of environmental effects) reflect these cultural forces and never simply an intrinsic or "natural" balance of nature versus nurture.

As a limiting case, let's imagine a future society that has reached a technological "singularity" that brings forth the rapid achievement of not only technological mastery, but also everlasting peace, spiritual enlightenment, and even distribution of resources. As a result, this society has managed to flatten out any environmental variation among its citizens, at least the kind of variation that impinges on standard outcome variables of behavioural genetic studies. Now, any phenotypic outcome in this society would be explained wholly by genes, since there is no longer any environmental variation left to regress onto. The citizens of this society are able to do things like hand-build quantum computers or fly space gliders via brain-embedded chips, but how meaningful is it to say that these abilities are 100% genetic? The information needed to construct these abilities is clearly going to reside in the cultural environment rather than be encoded in the genome. These abilities are explained wholly by genes in this society, but only because in our calculation of the genetic effect we abstract away the past trajectory of cultural change.

No matter how intuitive it may seem, the nature–nurture framework hardly "cleaves nature at her joints". It is, rather, a model that is useful for some purposes and unsuitable for others, but fundamentally restricted in the processes that it captures. Nature–nurture appears to be structured the same way as a certain kind of counterfactual thinking that involves questions along the lines of, "if she were born into a poor family, how would she have turned out?" Such thought experiments are intuitive for most people, and we might even say that people are generally fascinated by such developmental counterfactuals, as evidenced by the ubiquity of narratives that evoke them, ranging from Oedipus Rex to Cinderella to Star Wars. The problem of how much of a phenotypic outcome is due to birth and how much to upbringing is highly relevant when considering such questions, and it perhaps even serves as a way to roughly assess the degree of the potential manipulability of behavioural phenotypes were it possible to design rearing environments. All of this contributes to the seeming intuitiveness of the conventional nature–nurture framework. However, nature–nurture fails to serve as a productive instrument for scientific inquiry into the forces that shape the human psychological phenotype, due to our cultural inheritance.

Although naïve interpretation of genetic effects can conceal the cultural contribution to our psychological and behavioral phenotypes, other forms of observation help to unveil it. Documenting cross-cultural variation is one key approach, although the WEIRD people problem in the behavioral sciences has thwarted the collection of sufficiently diverse data for many years (Apicella et al., 2020; Barrett, 2020b; Henrich et al., 2010b). Only recently is this problem beginning to be slowly rectified. Another approach is improving our understanding of the plasticity of psychological phenotypes, and how it relates to culturally channelled environmental input. Plasticity has been given extensive treatment in the cognitive and brain sciences (e.g., Anderson, 2014; Frankenhuis & Nettle, 2020; Lövdén et al., 2010), but here we are interested in relating it to the population framework of cultural evolution. In doing so, we establish a conceptual integration between the individual-level notion of cognitive plasticity and the population-level notion of evolvability, and use the latter as a model for understanding the former.

The evolvable structure of cultural transmission

The notion of evolvability

Evolvability, as a general notion, refers to the ability of a system to undergo adaptive change. Alberch (1991) attributes the first use of the term in its current usage to Dawkins and Langton (1989). However, the term has since been used in several different ways; in a review of the literature on evolvability, Pigliucci (2008) distinguishes between three different but overlapping meanings of the term: The first meaning points to the standing genetic variance of a population, which in Fisher's fundamental theorem of natural selection (Fisher, 1930) serves as a measure of the responsiveness of that population to natural or artificial selection. More variance means more alternatives for natural selection to choose from. This sense of evolvability is roughly synonymous with heritability, and does not move beyond the insights that had already been developed within the Modern Synthesis[2].

The second meaning, attributed to the theoretical innovation of Wagner and Altenberg (1996), indicates not only realized genetic variation, but also the phenotypic variation that a population is capable of generating ontogenetically given its genetic material. In the framework of Wagner and Altenberg, this potential variation, or variability as they call it, is controlled by a "genotype–phenotype map" (G–P map). Epistasis[3] and canalisation[4] are two examples of phenomena that are determined by a G–P map: if an epistatic interaction between two genes is turned on or off by a third gene, the result is a change in phenotype despite the genotype remaining constant. Conversely, developmental canalisation is a phenomenon in which the realisation of an end-state phenotype remains stable despite genetic change (Hornstein & Shomron, 2006; Waddington, 1942). The G–P map is itself under genetic control, implying

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[2] The convergence of ideas stemming from Darwin, Mendel, and others within a mathematical framework, which occurred in the early 20th century and is often considered to be the establishment of the framework of modern biology.

[3] An interaction between genes that are not alleles, in which one gene suppresses the effect of another.

[4] A property observed in ontogeny, in which particular outcomes occur reliably even when preceded by deviations away from the expected developmental trajectory.

that the network of gene interactions that regulate the relative flexibility or rigidity of phenotypes is subject to natural selection and other evolutionary processes.

The third meaning of the evolvability is, according to Pigliucci, one in which the term is used to refer to the ability of a genome to generate major phenotypic innovations, such as those implicated in the Major Transitions of Maynard-Smith and Szathmary (1995). Evolvability in this sense is used to explain processes at the scale of phylogenetic divergence, in which novel phenotypes emerge and branch out to create new kinds of species. In the present discussion we will not be referring to evolvability in this sense.

Temporally contingent adaptation

Evolvability becomes critical when a population undergoes environmental flux and is required to adapt to novel selection pressures. Contrarily, in a totally stable environment, the greatest fitness payoff would go to organisms with the least amount of evolvability—the ones that have rigidified their phenotypic expression to precisely match the demands of that specific environment; any variation from this optimum would necessarily incur a cost. Evolvability, in its basic formulation, is thus characterized by an intrinsic trade-off, in which the benefit of being evolvable is dependent on the degree of expected environmental change.

However, the current characterization of evolvability assumes a fixed setting of the degree of phenotypic variability. One way to circumvent this trade-off would be to regulate variability in an adaptive manner. An evolved example of such a strategy is what Lindquist and colleagues have called "evolutionary capacitance" (Queitsch et al., 2002; S. Rutherford et al., 2007; S. L. Rutherford & Lindquist, 1998), which refers to the ability of some systems to accumulate genetic variation that is not reflected in corresponding phenotypic changes ("cryptic variation") and then subsequently reveal this variation phenotypically, in analogous fashion to how electrical capacitors store and release charge. The heat-shock protein Hsp90 has been proposed to serve as an evolutionary capacitor; in both fruitflies (Rutherford & Lindquist, 1998) and plants (Queitsch et al., 2002), it has been observed that this protein normally buffers phenotypes from the effect of genetic mutations, but gives way to elaborate morphological variation, some of which are potentially adaptive, once the organism is placed under challenging conditions such as high temperature during development. By being contingent on the detection of anomalous environmental conditions, a mechanism like capacitance can plausibly promote the adaptive regulation of phenotypic variability, or in other words tweak the G–P map (turn canalization on and off) in an environmentally responsive manner.

Adaptive regulation of variability need not necessarily depend on modifications of G–P mapping. A more primitive way of realizing the same kind of function has been observed in several species of bacteria, in the form of "mutator alleles" that promote increased levels of genetic and phenotypic mutation. Modeling studies suggest that despite the predominantly deleterious outcomes associated with genetic mutation, mutator alleles can be adaptive within fluctuating environments (Tanaka et al., 2003; Travis & Travis, 2002). There are also indications that the long-run fitness costs of a high mutation rate can be ameliorated by the presence of mechanisms that reverse the acquisition of mutator alleles, such as horizontal gene transfer from individuals that possess the wildtype non-mutator allele (Denamur & Matic, 2006; Taddei et al., 1997), or simply awaiting a counter-mutation that reverses the original emergence of the mutator allele. This reversion of the mutator allele, whatever the specific mechanism may be, parallels the switching on-and-off of variability-generating mechanisms described above, but the difference is that whereas evolutionary capacitance is contingently linked to environmental state, the use of horizontal gene transfer is, at least in its basic conception, a purely stochastic process. This is potentially significant because the latter case suggests that evolvability can be achieved using only the generic processes of mutation and natural selection, if occurring under the right conditions.

Dimensional adaptation

Thus far, I have been discussing evolvability in terms of increases and decreases in mutational rate, but the amount of mutation and its contingent regulation is not the only relevant attribute. Evolvability can also be structured along particular degrees of freedom that allow variability to have more adaptive effects than would be expected from purely random change. This point has been demonstrated in a simple mathematical model by Draghi and Wagner (2008). It also meshes with the theoretical paradigm proposed by Kirschner and Gerhart (Gerhart & Kirschner, 2007; Kirschner & Gerhart, 1998, 2005): they deploy a large body of evidence to advance the claim that the core physiological and developmental processes that emerged early in the evolution of multi-cellular animals, such as compartmented body plans and binary-like intercellular signaling, have been conserved since at least the early Cambrian (530 million years ago) in the entire metazoan clade—whose contemporary descendants range from jaguars to jellyfish—and that this is the case precisely because these core processes enable flexible adaptation to new environments, i.e., evolvability. By having constraints in organismal function imposed along these particular dimensions, animal phenotypes have been free to vary in other dimensions that have been selected to support adaptive fit with their environments: they possess appropriate variational structure. Therefore, exploration along fitness landscapes has been occurring not through purely random variation, as the proponents of the Modern Synthesis had initially imagined, but rather through the use of "facilitated variation" (Gerhart & Kirschner, 2007) as the authors call it, in which the basic mechanisms that generate phenotypic variation are themselves the conserved products of early evolution.

Modularity is another important concept that is related to facilitated variation, and in their theory, Gerhart and Kirschner (2007) treat it as one of the systemic properties that are enabled by the conserved core processes. Modularity refers to the property of systems that contain parts that are internally integrated but relatively autonomous with respect to other parts, or in other words, systems that can be analytically or functionally decomposed into naturally cohering sub-units (Simon, 1962; Wagner et al., 2007). Modularity affords evolvability because rather than having to build up complex structures from scratch, evolution is able to achieve this through combinatorial, hierarchical, or other kinds of generative processes that build on top of the complexity that is already realized in each sub-unit or module. Gene regulatory networks, brains, natural languages, and human organizations exhibit modular structure. There is evidence that modularity emerges as a result of selection pressure to reduce the cost of connections among network nodes (Clune et al., 2013).

Because almost all of the published literature on evolvability has concerned the genetic domain, in this summary of the concept, I have focused exclusively on how it relates to genetic variability. The goal, however, is to interpret how these mechanisms may be operating in the cultural domain.

Cultural evolvability

Culture plays a large role in the evolvability of the human phenotype, whether we are referring to the term in the sense of standing variation or configuration of the G–P map (i.e., Pigliucci's (2008) first and second meanings of evolvability, respectively). Whereas phenotypic variation in genetic evolution derives primarily from the biochemical process of nucleotide substitution (mutation) and related events such as failure in DNA repair, as well as the stochastic processes inherent in development, variation in cultural evolution is generated during the transfer of cultural traits. Cultural transmission can take many decades for skills such as hunting (Gurven et al., 2006a; Koster et al., 2020; Schniter et al., 2015c), opening up the transmission process to many potential sources of variation, and different social learning strategies result in different degrees of cultural variance (Henrich, 2001, 2004a). These are just some of the ways in which the generation of cultural variation differs from the production of genetic variation. Moreover, culture can also feed back onto genes, reducing genetic variation in the case of directional culture–gene coevolutionary selection (e.g., Beja-Pereira et al., 2003), but potentially also increasing genetic variation in other cases, such as when gene function is masked by cultural innovations (Uchiyama et al., forthcoming; ; Chapter 3 of this thesis). Culture can therefore modulate evolvability in culture itself, as well in the genome.

Authors such as Reader (2006), Sterelny (2006), and Wimsatt & Griesmer (2007) have discussed how we might use the concept of evolvability, along with associated frameworks such as evo-devo, to help us expand the scope of cultural evolutionary theory. Topics such as modularity and developmental constraints have been raised, along with a few cursory examples of how they might map onto cultural phenomena, but these attempts have been broad and abstract. Here I will take an approach that is more fine-grained, and allows us to transition into a neurophenotypic level of analysis.

Standing variation in the cultural domain

The first level of evolvability that we can look at is standing variation. Henrich (2004), in an influential model of cultural transmission with noise, demonstrated the important role of transmission variance in sustaining and improving the adaptiveness of a given cultural trait. The idea is similar to the role of mutations in genetic evolution: most noisy replicates of the model will be of poorer quality than the original but some will be better, and as long as learners in the subsequent generation possess the ability to home in on the best models, a noisy transmission process can be beneficial for the progressive improvement of the trait. Even this simple model demonstrates to us how we might expect different degrees of cultural variance across societies, depending on multiple factors such as the capacity for tolerating replication error, the size of the population, and the effectiveness of social learning strategies (Kendal et al., 2018; Rendell et al., 2011a), each of which may in turn depend upon environmental factors.

An examination of cultural psychology suggests what kind of traits may mediate cross-cultural variation in cultural variance. For example, Gelfand and colleagues argue that societies differ in the degree to which they tolerate deviation from social norms, and that this measure—*tightness/looseness*—correlates with various factors from personality measures to the prevalence of natural disasters and historical threats from neighboring societies (Gelfand et al., 2011a; Gelfand, 2018; Harrington & Gelfand, 2014). Underlying this framework is a functional argument, that societies have been selected for different degrees of tightness/looseness depending on the degree to which orderly social coordination had been valuable in their historical contexts, given their particular ecological and political contexts—greater turmoil and unpredictability increases dependence on norm-conformity or tightness. Because tightness/looseness regulates behavioral conformity, it is directly linked to cultural variability, where looser societies have more leeway for rapid adaptation to environmental change, and hence greater cultural evolvability in the sense of a greater amount of standing variation. On the surface, this hypothesis appears to stand in contrast to the argument that over the historical duration spanning ancient to modern European history, highly creative individuals have emerged more prolifically following periods of political and imperial instability (Simonton, 1975). However, this may be due to mechanisms that are separate from tightness–looseness, such as increased mixing between societies that were previously culturally disconnected.

Individualism/collectivism is another psychological dimension on which societies vary, and it indexes the degree to which the members of a society are psychologically more oriented toward the self and the immediate family or toward larger clusters of the in-group community

(Triandis et al., 1988). Although there is overlap with tightness/looseness as a construct, individualism/collectivism is not a direct measure of conformism. Much of the work in cross-cultural psychology has been comparison between Western and East Asian populations, and these studies have often shown that Asians tend to adopt, among other things, conformist and tradition-based patterns of behavior, whereas Westerners tend to lean more toward critical thinking and innovation.

Chang et al. (2011) present a causal hypothesis in which they argue that these differences in behaviour reflect a difference in the degree of weighting placed on social learning, and then relate this difference to long-term environmental variability between Western Europe and East Asia (primarily China), such that Europeans—who have historically undergone greater environmental variability along several factors such as migration, war, and changes in mode of subsistence—came to rely more on asocial (individual) learning whereas relative stability in East Asia led to an emphasis on social learning. In most models of cultural transmission, a greater reliance on social learning would imply less cultural variance, but pinpointing the true cause of variation in individualism/collectivism across groups will not be easy, due to the complex, multidimensional character as well as the historical depth of the problem. Note that even within countries, there is evidence of regional differences in individualism/collectivism (Kitayama et al., 2006; Talhelm et al., 2014; Uskul et al., 2008). These differences are often proposed to be related to differences in mode of subsistence, and the variation in the level of cooperation that they have historically required. Although subsistence-related cooperation may be correlated with social learning, this is certainly not a logically necessary outcome.

Cross-cultural psychological variation can explain part of the difference in cultural variance across societies as we have seen, but it is bound to be confounded with population structure to some extent. Some societies are more culturally fragmented than others. Whereas some populations are relatively homogeneous, with no salient clustering within the overall network of cultural transmission, others are densely clustered, due to the presence of partitions that weaken the links between subgroups. When these partitions are of a geographic or linguistic nature, they may be easily observed on the basis of standard social science data. When they are of a more sociological nature, such as gaps in class, wealth, or identity, these cultural partitions may be more difficult to observe. In some cases, when the partitions are of a more subtle nature, it make take great effort to even detect the presence of separated clusters. Social media may be one example of a non-traditional partition that can under some circumstances induce cultural clustering (Allcott et al., 2020; Asimovic et al., 2021; Bail et al., 2018; Urman, 2020). This kind of population structure, which Uchiyama, Spicer, and Muthukrishna (forthcoming; Chapter 3 of this thesis) refer to as the "hidden cluster problem", can induce cultural variance independently of psychological traits like tightness/looseness or individualism/collectivism.

Although there is uncertainty in the causes that drive it, societies clearly vary in their level of standing cultural variation. Whether these differences derive from psychology, population-structure, or random noise, it is necessary to better understand the dynamic processes that generate this cross-cultural variation in within-culture variation.

Cultural regulation of transmission parameters

Moving up one level of complexity from standing variation, let us consider how cultural variance is modulated endogenously by other cultural traits. This kind of catalytic factor coincides with what Acerbi, Ghirlanda, and Enquist (2014) call *regulatory traits*, or "traits that both regulate cultural transmission (e.g., from whom to learn) and are themselves subject [to] cultural transmission". The concept is fleshed out in a series of models that demonstrate the kind of dynamics that emerge when the traits transmitted through social learning influence a learner's tendency to engage in further social learning (Acerbi et al., 2009, 2012; Ghirlanda et al., 2006). As a central example, the authors discuss the trait of conservatism, which they define as relatively decreased openness to the adoption of new ideas and thus a reduction in social learning. In their models, conservatism spreads across a population because of an asymmetry in which open individuals are prone to adopting conservatism while the opposite does not hold.

Heyes (2012) pursues a similar argument as Acerbi and colleagues, interpreting empirical data from the domains of reading, social learning, and imitation as evidence that some cognitive processes are both constructed through cultural learning and also contribute to cultural learning in cyclic fashion. Heyes and Frith (2014) extend this approach to Theory of Mind as well (for an overview see Heyes, 2016).

These studies illustrate endogenous control of cultural learning by culturally learned traits. Mesoudi et al. (2016) positions this learning dynamic at one end of a continuum, where it constitutes the most complex form of plasticity of social learning. On this continuum, less plastic species follow social learning patterns that vary as a function of genetic polymorphisms, and intermediate species are able to switch their social learning patterns in response to non-cultural environmental cues. For social learning in humans, culturally mediated plasticity in social or cultural learning is likely to be a significant property of our learning profile. If cultural input is able to transform cultural transmission, this may serve an explanatory role in why human culture has reached the level of complexity that it has.

We may attempt to make a provisional distinction between transformations that affect the quality of the input that can be obtained through cultural learning, or *channel regulation*, and transformations that affect the distribution of the input across different potential models, or *network regulation*. As an example of channel regulation, controlled experiments show that verbal instruction improves transmission fidelity in transmission chains of stone-tool making (Morgan et al., 2015). Language in this case is a technology that transforms cultural transmission by impacting the quality, but not necessarily the distribution. In contrast, social norms that promote interaction with extended kin would be an example of network regulation. An increase in the number of models may also be associated with an improvement in the quality of cultural transmission due to reduction in noise (Henrich, 2004a; Muthukrishna et al., 2014), but this is not necessarily the case—if broad learning from many models is substituting targeted learning from a known expert, this could be a trait that transforms the distribution but not the quality (or degrades the quality) of cultural transmission. The focus of Heyes and colleagues (Heyes, 2012, 2018; Heyes & Frith, 2014) is on channel regulation, whereas the focus of Acerbi and colleagues (Acerbi et al., 2009, 2012; Ghirlanda et al., 2006) is on network regulation.

Claidière and André (2012) argue that while there is utility in modeling genetic transmission due to its intelligible structure, the transmission mechanisms of cultural evolution are so fluid, multifarious, and contingent on extrinsic variables that the very attempt to study culture using an evolutionary modelling cannot be a viable endeavor. However, fluidity, multiplicity, and contingency are all properties to be expected if cultural transmission is regulated by cultural input, in the manner illustrated by the studies that we have reviewed here. The upshot of Claidière and André's suspicion may be less about whether evolutionary models are the right tool for cultural transmission, and more about how we need to account for this additional layer of complexity in cultural evolution research as a baseline, at least for human and other species with significant levels of plasticity in cultural learning. At the least, this complexity is likely to play a key role in explaining human cultural evolution in particular.

The broader picture here concerns not the effect of particular traits such as conservatism or theory of mind, but rather how evolvability is implemented within the cultural domain as a whole. From the very beginning evolutionary biologists have been considerably less adept at explaining variation than they have been in explaining the other two "ingredients" of adaptive evolution: inheritance and differential reproduction. Darwin provided the original insight about natural selection and molecular biology supplied the mechanisms of inheritance, but the question of how genetic mutation gives rise to effective phenotypic variation has been more enigmatic (Kirschner & Gerhart, 2005), and the concept of evolvability hovers over this theoretical lacuna. Being a subfield of evolutionary biology, cultural evolution has to some degree inherited this imbalance in explanatory capacity, being more successful in explaining the mechanisms of selection and inheritance than in explaining the production of variation. Evolvability is thus likely to be an area of significant promise in cultural evolutionary research.

The notion of cultural evolvability describes how modulation of cultural transmission influences the flexibility with which societies can adapt to changing environments. What we want to know is how these changes to the network structure of cultural transmission translate into phenotypic change, in particular neurophenotypic change. Cultural evolution of psychological traits ultimately hinges upon the interface between the brain and environmental input. A focus on this interface is essential for deepening our understanding of how the population dynamics of cultural evolution reach into the internal structure of our brains and minds.

Cultural evolution of brains and their environments

Because the cultural evolutionary framework has its roots in anthropology, the focus has often been on ethnographically salient behavioural traits like tool-making and rituals, but there is nothing about the formal framework that limits it to examples such as these. Although we do not yet know the magnitude of the effect nor even how to reliably measure it, the collective process of cultural evolution is likely to have a significant role in shaping many if not most aspects of human psychology and behaviour. Cultural transmission transmits not just discrete traits, but whole environments (i.e., the totality of inputs to phenotypic development that are not attributed to genes, following the usage of the term "environment" in behavioral genetics and developmental science). By conceptualizing cultural transmission as the transfer of arrays of environmental exposure, we align cultural evolutionary theory more closely with developmental science and facilitate a closer integration of the two fields (c.f., Bronfenbrenner & Ceci, 1994; Gottlieb, 2007). This integrated cultural–biodevelopmental approach guides us toward the proximal mechanisms that support cultural evolution. It furnishes a conceptual lens through which we may observe the ways in which cultural dynamics exploit various degrees of freedom in proximal mechanisms, and thus inevitably brings us to a closer examination of the interface of cultural evolution and brain development.

Culturally channelled inputs to brain development

Neural architecture places strong constraints on the cultural traits that can be acquired, and by doing so shapes the population distribution of cultural traits. For example, take reading. The patch of neocortex selectively involved in reading, the VWFA (visual word-form area), is a left-hemisphere inferior-temporal visual region that is suited for making fine discriminations between line configurations that are projected onto the fovea[5]. Its response properties conform appropriately to the hierarchical processing architecture of the ventral visual stream[6] within which it is situated (Vinckier et al., 2007). The ventral visual stream is an architectural feature shared with other primates (DiCarlo et al., 2012; Rajalingham et al., 2020)—there is nothing

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[5] the receptor-dense notch at the center of the retina that affords high-acuity vision

[6] An information processing pathway that passes through the bottom side of the mammalian neocortex, which is associated with tasks such as object recognition

phylogenetically remarkable about the organization of the VWFA, although reading and writing are behaviours only found in humans. What is remarkable is not how the brain is adapted to writing, but conversely, how writing is adapted to the brain. For instance, thorough examination of multiple writing systems with independent cultural origins reveals significant overlap in the type of line configurations that tend to appear across these writing systems, and these recurring configurations also match the statistics of line configurations that occur in photos of the natural world (Changizi et al., 2006; Changizi & Shimojo, 2005).

Because writing was only invented in the last few thousand years, the slow process of genetic evolution cannot explain this tight structural fit between the shape of letters and the properties of the VWFA. The best explanation is perhaps what Dehaene and Cohen (2007) call "neuronal recycling"—the process by which a cultural invention finds its neural locus by taking over areas that were previously selected for evolutionarily older functions, thereby inheriting the information-processing constraints of their predecessors. There are two sides to neuronal recycling, or rather, two adaptive processes that enable it. Cultural evolution is one—it is the process that iteratively reshapes the input characteristics of cultural traits so that they converge upon a computational fit with the response profiles of extant cortical areas. At the same time, cortical areas also undergo functional differentiation and specialization over the course of development, adapting their computations and response profiles to the input they are exposed to. This is known as interactive specialisation (M. H. Johnson, 2000, 2011), and is the other process that enables neuronal recycling to achieve a good fit between neocortex and world. Alignment of brain and culture is supported by cultural evolution occurring over generational time scales and interactive specialisation occurring over developmental time scales.

Representations of written symbols settle in the VWFA, but in the absence of orthographic input during early development, this area is devoted to visual discrimination of faces. Learning to read involves large-scale cortical reorganization where face-processing becomes shunted from VWFA into the opposite, right, hemisphere, and also modifies the encoding of phonemic representations that occur in associated auditory areas (Dehaene et al., 2010). This contrast in neural organization between brains exposed to written symbols and those that are not hints at the power of interactive specialization, and development in general. Interactive specialisation sorts representational loci on the basis of fit between area-specific response profiles and the incoming flow of sensory input. This is a self-organising process[7], but one with much precision in the matching of cultural inputs to cortical loci. For example, the topographical organization of white matter connectivity prior to literacy acquisition predicts the specific location where the VWFA will emerge years later (Saygin et al., 2016). At the same time, there is a substantial literature on cortical plasticity, for example how visual cortex can be recruited for the discrimination of braille in the blind, and how auditory cortex can be repurposed for interpretation of sign language for the deaf (Merabet & Pascual-Leone, 2010; Sadato et al., 1996). Neural development thus simultaneously exhibits remarkable flexibility and long-range stability. It can respond contingently to environmental inputs but do so in a highly predictable manner.

Reliability of outcome of the VWFA despite this intrinsic flexibility in organization suggests that the structure and function of VWFA appears stable and invariant in neuroimaging studies only because the input that drives the outcome is stable and invariant. In the kind of societies (and sub-groups within societies) from which neuroscience data are commonly collected, written symbols are indeed a largely invariant input due to the form of its cultural transmission. Formal literacy instruction is imparted through standardized education, and much of the informal exposure to this domain of input is found in visual and print media that are widely available to the point of being ubiquitous. However, this uniformity of exposure is clearly not present everywhere on the globe. Rates of literacy vary, but so do the shapes of the cultural transmission networks that deliver contact with written symbols. Even in societies where exposure is uniform today, the transmission networks would have looked very different just a few centuries or even decades ago. The apparent stability of VWFA organization is thus at least partly the outcome of a WEIRD (Western, educated, industrialised, rich, democratic) sampling problem in human cognitive neuroscience (Chiao et al., 2013; Uchiyama & Muthukrishna, in pressa) as well as the unavoidable bias toward contemporary populations (Muthukrishna et al., 2021a).

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[7] not pre-specified and instead arising through the interaction of simpler, lower-level component processes

Although most neuroimaging studies are conducted in societies that adopt variations on the Roman alphabet, other societies use different writing systems, which can reveal systematic differences in neural representation. For example, when comparing to English orthography, acquisition of Chinese orthography is associated with increased recruitment of more intermediate visual areas, as well as recruitment of the right hemisphere[8] (Perfetti et al., 2013; Wu et al., 2012). Differences in the morphological properties of Chinese and English characters also have downstream effects in domains beyond reading itself. For example, due to properties of Chinese characters such as the density of visual features as well as its high information-content with respect to the entire distribution of symbols, visual ability and manual writing skill predict reading proficiency in Chinese children more than they do in Western children (Koyama et al., 2011; Tan, Spinks, et al., 2005; Yang et al., 2013). In the reverse direction, acquisition of literacy may also play a causal role in the improvement of visual ability in Chinese-reading children but not in Western children (Demetriou et al., 2005; McBride-Chang et al., 2011), setting up feedback mechanisms between cultural exposure and neurophenotypic development that diverge between the two cultures.

The contrast between English and Chinese orthography is one example of how variation in input shapes variation in brain organisation. Cross-cultural neural variation (typically documented between Western and East Asian societies) has been observed in other domains such as visuo-spatial judgment (Goh et al., 2013), self-reflection (Chiao et al., 2009; Ma et al., 2014), and empathy (Cheon et al., 2011). However, the developmental processes and exposures that engender cross-culturally divergent traits within these more complex domains are less well understood than in the case of reading, a relatively tractable phenotype. Such complex cultural divergences are likely to be attributed not just to differences in raw sensory exposure between groups, but also to variation in the interpretation of experiences as shared by caretakers through joint attention and discourse, in a culture-specific fashion (Senzaki et al., 2016; Wang, 2001). But the words, concepts, theory of mind, and parenting approaches required to engage in this kind of shared experience do not emanate from the caretaker intrinsically, but are rather the products of cultural evolution.

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[8] Orthographic processing for the English alphabet is characterized by greater activation of early visual areas and restricted to left hemisphere activation. The VWFA is an area localised to the left hemisphere.

Cognitive evolution powered by cultural evolution

Neural evolution is almost always discussed in terms of genetic evolution, but there is conceptual clarity to be gained by recognising that genes and culture can both modify brain organization and function. In doing so, we extend dual inheritance (Boyd & Richerson, 1985) into an analysis of brain development. On the face of it, this parallel may appear like a false equivalency. Culture-driven neural change is limited—most of brain development is grounded in a systematic sequence of morphogenetic events that unfold like clockwork, all the way from the formation of neural tube in the embryo to prefrontal maturation into adulthood (Puelles et al., 2013; Workman et al., 2013b). The basic elements of neural architecture are prepared through this deeply phylogenetically conserved process, and there is virtually no scope for any kind of experience to intervene in this process constructively, only as disruption (e.g., exposure to toxins or physical insults).

However, the same can be said of genetic change. For a highly conserved and developmentally critical process like segmentation of the body plan or embryonic brain development, the vast majority of genetic mutations are deleterious by necessity. When a genetic mutation does successfully bestow adaptive function, it will typically be expressed along particular domains of variation or "movable parts" that support the evolvability of the nervous system (Kirschner & Gerhart, 2005). Finlay and colleagues (Anderson & Finlay, 2014; Finlay et al., 2011) propose three such levers for the nervous system: (1) changes to the sensory or motor periphery inducing coordinated changes in the central nervous system, (2) changes to the distribution of neuromodulators and their receptors inducing motivational changes with respect to the social world, and (3) reallocation of brain areas or networks of areas to non-normative types of input, such as the use of visual cortex for reading braille.

Culture is also likely to achieve its impact by tweaking particular domains of variation. However, these points of flexibility will not necessarily be intuitive. For example, an infant's visual field is populated with different objects that come and go, and it is not only the category of the objects that appear, but also the skew in the distribution of their frequencies of appearance that changes as a function of age (Clerkin et al., 2017; Smith et al., 2018). These transitions are due not only to improvements in motor ability but also to changes in the behaviour of caretakers. Particular longitudinal patterns of visual exposure such as these may facilitate normative outcomes in domains such as visual ability and word learning, where these patterns naturally solve the problem of "curriculum learning"— a methodology in machine learning for optimising the sequence and distribution of learning stimuli (Bengio et al., 2009)— according to Smith and colleagues (2018). Therefore, when children in different cultures superficially appear to be exposed to the same inputs, this impression of sameness may belie differences such as the order and distributions with which they are presented—differences that have long been known to impact learning outcomes in neural networks models of cognitive development (Elman et al., 1996). Subtle forms of developmental structure in sensorimotor input may have cumulative downstream impact on developmental outcomes. This view opens up the search for possible sources of variation in experience that are opaque to conventional methods but potentially recoverable from innovations in data collection.

Just as cultural evolution can explore the space of possible tools by incrementally generating variation in tool-making procedures (Boyd et al., 2013; Henrich, 2004a; Kline & Boyd, 2010), cultural evolution can also explore the space of possible neurophenotypes by tweaking environmental input to the brain [9] . On the one hand, the subspace of neurophenotypes accessible by culture is likely to be limited in reach compared to genes, as genes can tweak the brain from the inside in ways that culture cannot. On the other hand, the set of possible environments that can be generated by cumulative cultural evolution is enormous—what it generates are not just momentary exposures but rather longitudinally extended structures of developmental input that can be coordinated with stages of brain development such as sensitive periods. Moreover, cultural exploration of neurophenotypic space occurs much more rapidly than the time scale of genetic change.

Because the production of neurophenotypic variation is regulated by both cultural and genetic change, neural evolvability is coupled to both. Because cultural evolutionary dynamics are dependent upon population parameters such as population size, network structure, and variability, human neurophenotypes are produced and regulated by collective processes. From

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[9] Although knowledge of how to make a particular tool is also a neurophenotype in a trivial sense, we focus here on broader changes in functional organization that have effects on cognition and behaviour outside of the domain of the original input.

this population vantage point, we are able to reinterpret classic concepts in psychology and cognitive science.

For example, take the notion of *learnability*, which is the degree to which some non-trivial mental representation, such as a grammar, can be extracted from ambiguous input (Pinker, 1989). Many key disputes within cognitive science have revolved around the issue of learnability—for example whether human learning is built from domain-specific or domain-general learning systems (Elman et al., 1996; Fodor, 1975; Rumelhart et al., 1986) whether language learning requires innate computational structures (Chomsky, 1959, 1965; Christiansen & Chater, 2016a; Pinker, 1984; Skinner, 1957), or whether past evolutionary selection can explain some of the puzzling aspects of human thought (Tooby & Cosmides, 1992).

The issue of learnability is typically analysed through the lens of the average-case scenario. But from the perspective of population dynamics, the effect of the average input on the average learner is less important than the effect of the entire distribution of inputs on the entire population of learners. In a population, learners will vary in which inputs they find more learnable. The magnitude of this variation in learnability will depend upon both the variation in organic traits (roughly aligned with genetic variability but also shaped by previous experience, e.g., experience-dependent changes in white matter structure) and the variation in inputs to be learned. Where there is both little organic variation and little variation in inputs, variation in learnability will be correspondingly small. Where there is large organic variation and large variation in inputs, variation in learnability will be large. At the individual level, low learnability suggests a poor outcome. At the population level, low mean learnability suggests a poorer mean outcome but possibly also greater variation in the outcomes of learning. Models of cumulative cultural evolution show that variability of acquisition is a crucial component of innovation and of cumulative cultural evolution (Henrich, 2004a; Muthukrishna & Henrich, 2016a). Therefore, under certain conditions, a steep gradient of learnability may facilitate rapid cultural adaptation, or in other words evolvability.

Long division, counting on fingers, written records of debt, metrical poetry, the method of loci—each of these is an example of a cultural practice that may have plausibly originated as a method for the compensation of cognitive deficiencies. By tweaking the form of a cultural practice (or a physical artifact), the computational load borne by internal thought can be partly offset onto the practice or artifact, a process referred to as “cognitive offloading” or “distributed cognition” (Hutchins, 1995; Kirsh, 2010; Risko & Gilbert, 2016; Zhang & Norman, 1994). Dor and Jablonka (2010) propose that grammar itself arose from a similar condition, where a minority of individuals who were deficient in their ability to comprehend the semantics of primordial utterances introduced linear order as a means to facilitate the decoding of meaning. More generally, neurodiversity may breed innovation. In this manner, a population perspective on the construction of mental practices can help us understand how function gets built into the human psychobiological machinery.

Conclusion

The nature–nurture framework follows the standard model of the psychological sciences in adopting the ontology of the individual mind, whereas cultural evolution is organized around a population-based framework. All of the discrepancies between the two frameworks described thus far stem from this basic theoretical gap between the individual or agent and the population or collective. Over many years, enormous resources have been devoted to the study of how genes and environment influence psychological development: there is clearly widespread recognition that in order to understand the mind, we need to understand the formative processes that generate it. Although the developmental environment appears to be situated causally upstream within this formative dynamic, the developmental environment is itself the outcome of a higher-order formative dynamic that is powered by collective dynamics operating over many-generational time scales. The standard approach to nature–nurture theoretically truncates this loop: a collective dynamic is reduced to the relationship between an individual and its environment; trans-generational inheritance is reduced to a single iteration of ontogeny; a developmental outcome that can contribute to subsequent generations of learners is evaluated solely with respect to its desirability for the individual. By re-establishing this formative loop that runs seamlessly through the individual, the collective, and the developmental environment, we obtain insights into the organisation of human psychobiology—for example how cultural distributions produce variation and function for genomes and brains, both bearers of environmental information. Through substantive integration with the cultural evolutionary framework, the psychological sciences become able to simultaneously make sense of both individuals and societies in one sweep of the brush, rather than severing them into separate explanatory systems.

Chapter 3: Cultural evolution of genetic heritability

Abstract

Behavioral genetics and cultural evolution have both revolutionized our understanding of human behavior—largely independent of each other. Here we reconcile these two fields under a dual inheritance framework, offering a more nuanced understanding of the interaction between genes and culture. Going beyond typical analyses of gene–environment interactions, we describe the cultural dynamics that shape these interactions by shaping the environment and population structure. A cultural evolutionary approach can explain, for example, how factors such as rates of innovation and diffusion, density of cultural sub-groups, and tolerance for behavioral diversity impact heritability estimates, thus yielding predictions for different social contexts. Moreover, when cumulative culture functionally overlaps with genes, genetic effects become masked, unmasked, or even reversed, and the causal effects of an identified gene become confounded with features of the cultural environment. The manner of confounding is specific to a particular society at a particular time, but a WEIRD (Western, educated, industrialized, rich, democratic) sampling problem obscures this boundedness. Cultural evolutionary dynamics are typically missing from models of gene-to-phenotype causality, hindering generalizability of genetic effects across societies and across time. We lay out a reconciled framework and use it to predict the ways in which heritability should differ between societies, between socioeconomic levels and other groupings within some societies but not others, and over the life course. An integrated cultural evolutionary behavioral genetic approach cuts through the nature–nurture debate and helps resolve controversies in topics such as IQ.

Introduction

Business is booming in behavioral genetics. We're in the midst of a genome-wide association gold rush (Visscher et al., 2017). The availability of powerful computers and sequenced DNA of millions of people has led to an industrious search for single nucleotide polymorphisms (SNPs) that correlate with a variety of psychological and behavioral traits (Harden & Koellinger, 2020; Horwitz et al., 2019; Mills & Tropf, 2020). These range from memory capacity (Papassotiropoulos et al., 2011), cognitive ability (Coleman et al., 2019) and educational attainment (Lee et al., 2018) to moral attitudes (Brandt & Wetherell, 2012), political orientation (Hatemi et al., 2011), temporal discounting (Sanchez-Roige et al., 2018), socio-economic status (Hill et al. 2016), temperament (Zwir et al., 2018), and happiness (Wingo et al., 2017). The significance threshold for discovering correlations is high (a typical threshold being $p < 5 \times 10^{-8}$; Fadista et al., 2016) and there are claims that the curse of reverse causality has been lifted. As Plomin and von Stumm (2018) put it, genome-wide polygenic scores "are an exception to the rule that correlations do not imply causation in the sense that there can be no backward causation… nothing in our brains, behavior or environment changes inherited differences in our DNA sequence."

The last two decades have also seen a parallel revolution in cultural psychology and cultural evolution that has identified significant cultural variation in our psychology and behavior (Henrich, Heine, and Norenzayan 2010; Nisbett 2003; Muthukrishna et al. 2020; Henrich 2016; Muthukrishna and Henrich 2019; Gelfand 2018). These range from fairness and prosocial norms (Henrich et al., 2010b; Schulz et al., 2019) and attribution of blame (Barrett et al., 2016) to perceptual style (Kitayama et al., 2003a), susceptibility to visual illusions (Henrich et al., 2010b), visual perception more broadly (Lupyan et al., 2020), numeric chunking (Domahs et al., 2010), interpretation of linear and logarithmic numeric scales (Dehaene et al., 2008), neural correlates of reading (Bolger et al., 2005b; Tan, Laird, et al., 2005b), event segmentation (Swallow & Wang, 2020a), memory (Amici et al., 2019; Guida et al., 2018; Wang, 2021), spatial cognition (Majid et al., 2004), motor development (Karasik et al., 2015), folkbiology (Medin & Atran, 2004; Waxman et al., 2007), and personality (Gurven et al., 2013; Smaldino et al., 2019). Cultural evolution is part of a broader theoretical framework—dual inheritance theory (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) [10]—that incorporates genes, environment, culture, and learning to offer an explanatory and predictive framework for human psychology and behavior (Muthukrishna & Henrich,

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[10] Research within this framework also falls under culture-gene coevolutionary theory and the extended evolutionary synthesis (Laland et al., 2015a).

2019b). This body of research suggests that humans not only have a genetic inheritance from their parents, as do all animals, but also a substantial cumulative cultural inheritance from their societies, well beyond any culture found in other primates, birds, and whales (Dean et al. 2014; although also see Whiten 2019). Genes, culture, and the environment have often co-evolved, shaping our species (Henrich 2016; Laland 2018).

The revolutions in behavioral genetics and cultural evolution have occurred largely independently of each other. Some attempts have been made to integrate the fields (e.g., Laland, Odling-Smee, and Myles 2010; Creanza, Kolodny, and Feldman 2017; Feldman and Ramachandran 2018; Cavalli-Sforza and Feldman 1973; Cavalli-Sforza et al. 1982), with these efforts typically being launched by researchers in cultural evolution. As a result, cultural evolution has incorporated some aspects of behavioral genetics. Behavioral genetics in turn has been largely agnostic with respect to cultural evolution, which is perhaps understandable given the focus, size, and historical trajectory of the field. However, given the extensiveness of the cultural and culturally-shaped environment, cultural evolution offers an important but typically missing complement to otherwise insightful methodological and empirical analyses within behavioral genetics (e.g., Brumpton et al. 2020; Young et al. 2019; Turkheimer, Pettersson, and Horn 2014).

The effect of culture in behavioral genetics is typically incorporated into a broad environmental term that is partitioned into between- and within-family variance components. While behavioral genetic research implicitly or explicitly incorporates an understanding of the way in which genetic evolution shapes genotypes, the environment—cultural or otherwise—is assumed to be exogenous or at best shaped by genes (Plomin et al., 1977; Rutter, 2007). The environment is treated as given, while the genome is at least implicitly understood through the lens of selection and function. But just as genetic evolution offers a systematic framework for understanding how distributions of alleles change over time, cultural evolution offers a framework for understanding how distributions of cultural traits change over time; both evolving in response to ecological, demographic, and social factors. Thus, an understanding of cultural change can provide insights into the structure and dynamics of the environmental component of phenotypic variation as well as their interaction with genes. Statistical and theoretical models of gene-environment interactions and correlations are well-trod territory

(Plomin et al., 1977; Purcell, 2002; Rutter, 2007), but these models do not capture the cultural evolutionary dynamics of environmental change nor the coevolutionary dynamics of gene–culture interactions and correlations.

Humans have long been evolving in ways that deeply intertwine genes and culture: a prominent example is that we have jaws too weak and guts too short for a world without controlled fire and cooked food (Aiello & Wheeler, 1995a; Wrangham, 2017); we lack genes for fire-making or cooking, instead relying on culture to compensate. This kind of coevolutionary history renders some aspects of gene-culture or gene-environment interactions puzzling when taken outside of a dual inheritance framework. Such insights help with interpretation of data. For example, it is well understood and also statistically obvious that reducing environmental variation will increase heritability scores (Stoolmiller, 1999). What's less obvious is the way in which culture can either mask or unmask genetic variation, and the way in which cultural diffusion and innovation can increase or decrease heritability. It's similarly not obvious how to define a single society for the purposes of measuring heritability, without being able to identify cultural cleavages that can lead to Scarr-Rowe type effects (see Section 4.1; Turkheimer et al. 2003; Tucker-Drob and Bates 2016). Our goal is to offer a path to reconciliation between behavioral genetics and cultural evolution with new or complementary interpretations for various puzzles, such as differences in heritability between and within populations, differences in heritability across development, and the Flynn effect. In doing so, we hope to instigate a discussion that nuances common interpretations of the nature and nurture of human behavior.

Interpreting heritability

Heritability is an important metric in behavioral genetics. In its standard formulation, heritability refers to the proportion of phenotypic variance for some trait that is explained by genetic variance. Much has been written about the misunderstandings and pitfalls that commonly occur when interpreting heritability (e.g., Lewontin 1974; Vitzthum 2003; Visscher, Hill, and Wray 2008; Haworth and Davis 2014), and we will not recapitulate these arguments here except when necessary. Suffice to say, heritability is sometimes incorrectly treated as an index of the genetic basis of a trait, and hence as a measure of the relative contribution of nature vis-à-vis nurture.

Cultural evolutionary theory can contribute to our understanding of the interpretation of heritability by describing the processes of cultural transmission and cultural change. In standard treatments of heritability, phenotypic variance is partitioned into a component explained by genetic variance and a component explained by environmental variance. We will further conceptually partition this environmental component into a sub-component whose distribution is shaped by cultural transmission (the cultural environment or culture) and another whose distribution is not (the ecological environment or ecology). For the purposes of exposition, we will treat these as separable, though of course this dichotomization is merely an approximation as any sharp separation between the two is in reality implausible (Laland et al. 2015).

An example: skin pigmentation and UV

Before we unfold the complexities of interpreting the cultural evolution of genetic heritability, let’s begin with a simple illustration that introduces some basic concepts in both behavioral genetics and cultural evolution: the heritability of cancers associated with skin pigmentation. Genes affect the level of skin pigmentation and propensity for tanning instead of burning (Crawford et al., 2017). These are ancestral adaptations to levels of UV radiation at different latitudes (Barsh, 2003; Sturm & Duffy, 2012). Darker pigmentation protects against high levels of UV radiation, such as near the equator. Lighter pigmentation enables vitamin D synthesis in low levels of UV radiation, such as at Northern latitudes (Jablonski and Chaplin 2010; 2017). It is important to get the correct amount of UV radiation—too much causes skin cancer, but too little causes vitamin D deficiency, which is associated with other health problems (Edlich et al., 2009; Garland et al., 2006).

Worldwide migration has led to people with skin pigmentation mismatched to the level of UV radiation: Australians with European ancestry have higher rates of skin cancer than Australian Aboriginals and other non-European populations (Australian Institute of Health and Welfare, 2016), and conversely, Europeans with African and South Asian ancestry have higher rates of vitamin D deficiency and associated afflictions (Cashman et al., 2016; Spiro & Buttriss, 2014). A gene by environment interaction (G×E) approach could measure how these mismatches affect the heritability of skin cancer or vitamin D concentrations, but not how we should predict these heritability estimates to change over time through cultural evolution, specifically through diffusion and innovation. Through cultural evolution, non-genetic adaptations evolve to compensate for genetic mismatches: fairer Australians wear sunscreen, a hat, and covered clothing (Montague et al., 2001)[11], while darker Europeans consume vitamin D supplements and vitamin D-rich or fortified foods (Spiro & Buttriss, 2014).

In this example, the challenges to measuring and interpreting heritability and understanding GWAS results are perhaps more obvious than for many psychological traits. The heritability of skin cancer, for example, should be highest when there is more diversity of skin pigments (genes), more homogeneity of cultural practices (culture), and high UV radiation (ecology)[12]; see Figure 3.1. While ecology and genes may change to some degree (e.g. smaller hole in the ozone layer and immigration, respectively), cultural change can be particularly fast and potent—greater uptake of anti-skin cancer practices and technologies or new medical interventions for treating cancer. In some cases, cultural evolution is broadly predictable due to directionality—few are working on ways to *increase* rates of skin cancer. Of course, there may be other forces that work in the opposite direction, such as a tan becoming associated with attractiveness[13]. Here it is easier to see that heritability is a function not only of genes, traits, and ecology, but also of a cultural environment that is evolving according to dynamics that can be understood. The environment of the genome is therefore not an inert backdrop against which genes should be evaluated, but rather, a moving reference frame that rapidly evolves in relation to both genes and ecology.

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[11] Australia's Slip! Slop! Slap! campaign encourages practices to reduce UV radiation exposure: "slip on a shirt, slop on sunscreen and slap on a hat". More recently, it has been followed by the SunSmart program, which expanded upon the original message to further decrease exposure: "seek shade or shelter, and slide on sunglasses".

[12] An analogous case can be made for vitamin D deficiency, which should be highest under the same circumstances, except that instead of high UV, it should be low UV levels that most reveal the genetic effect.

[13] Many potential forces may contribute to this: prestige bias creates trends—historically, prior to the 1920s, tanning was associated with working in a field, but after Coco Chanel was sunburnt whilst holidaying in the French Riviera, her fans are said to have copied her tan; success bias as tanning is associated with more time for outdoor leisure; or simply some version of runaway cultural selection (Boyd & Richerson, 1985).

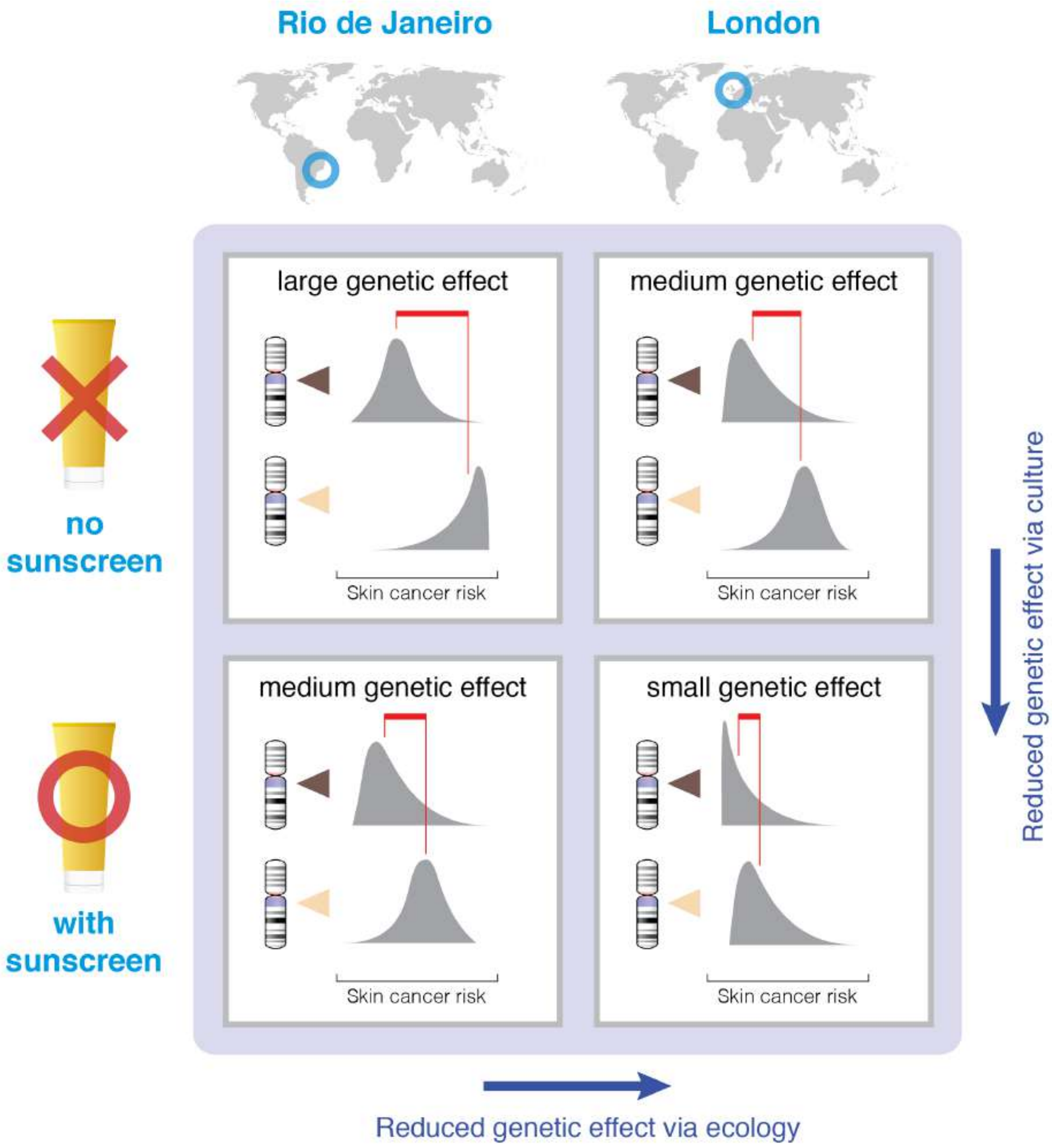

Figure 3.1: An illustration of the effect of sunscreen and geographic location on the effect size of a skin pigmentation gene with respect to skin cancer risk. The largest genetic effect should be found in societies that lack sunscreen and reside in locations with high levels of UV radiation (top-left square). Genetic effects should be reduced with either the introduction of sunscreen or residence in a lower-UV environment, both factors that mask the effect of skin pigmentation (bottom-left and top-right squares, respectively). The smallest effect should be found in societies that have both low UV and sunscreen (bottom-right square). Each cell represents a hypothetical scenario—if Rio and London did or did not have sunscreen. Chromosomes with dark indicators represent genes for strong pigmentation, and those with light indicators represent genes for light pigmentation. Gray distribution represents population distributions for skin cancer risk, and red lines point to the mean of each distribution.

This example helps us understand four key points. The first of these is well understood by behavioral geneticists and the second is sometimes noted, but the third and fourth points are typically absent from these discussions due to the disconnect between behavioral genetics and cultural evolution. First, there is no overarching, one-quantity heritability of a trait to be discovered. There is no fixed answer to the question, "What is the heritability of skin cancer?". Second, this answer will depend not only on ecology, but also on culture and specifically on cultural diffusion and innovation—both of which can rapidly change and therefore rapidly change heritability estimates. Third, the diffusion and innovation are broadly directional[14]. Cultural diffusion of sunscreen, clothing, shade and sunglasses, and cultural innovation toward more effective screening and treatment of melanomas all work to reduce heritability estimates. In these cases, we expect a reduction in heritability due to the masking effect of the cultural trait. Were any of these an example of culture unmasking genetic effects, such as tanning salons that induce differential risk according to skin pigmentation level, we would have predicted an increase in heritability. Insofar as a preference for avoiding some outcome outweighs other forces that tend to bring it forth, there will be a directional trend over time, similarly to directional selection in genetic evolution (Byars et al., 2010; Sanjak et al., 2018). Fourth, we might also expect the cultural response to be stronger where the ecological and cultural selection pressures are stronger—skin cancer mitigation in Australia but vitamin D supplementation in northern Europe. Heritability or changes in heritability of these cases have not been tested to our knowledge, but the predictions are clear.

Like heritability, the question "Which SNPs are associated with skin cancer?" is similarly culturally dependent. In societies where sunscreen use is common, we expect SNPs associated with skin pigmentation to be less predictive of skin cancer compared to societies where this is not the case. Similarly, we would expect SNPs associated with antioxidant metabolism (Oskina et al., 2014) to be less predictive of skin cancer in societies whose foods are rich in antioxidants—such as in traditional Mediterranean cuisine (Visioli & Galli, 2001).

That heritability is affected by the environment is widely understood (Feldman and Ramachandran 2018; Hamer and Sirota 2000; Moore and Shenk 2016; Turkheimer, Pettersson, and Horn 2014; Vitzthum 2003; Tenesa and Haley 2013; Charmantier and Garant

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[14] When the cultural forces are well understood, this directionality may be analyzable. And of course, not all cultural forces are adaptive. As in genetic evolution, some may be maladaptive (e.g., female genital mutilation; Efferson, Vogt, and Fehr 2020; Howard and Gibson 2017), mismatched (the Western diet causing disease; Cordain et al. 2005), neutral, or somewhere between these.

2005; Haworth and Davis 2014). And researchers like Lewontin and Feldman (Feldman & Lewontin, 1975; Lewontin, 1970, 1974) long ago described the fallacy of extrapolating heritability scores from one population to another. Their argument was made from the standpoint of gene-environment interactions: genetic effects must be understood in the environmental conditions under which the genes are expressed. In this target article we build on this rich body of research to launch a discussion of how the cultural environment changes over time and affects heritability—that is, the cultural evolution of genetic heritability (we schematically capture some of these key ideas in Figure 3.2).

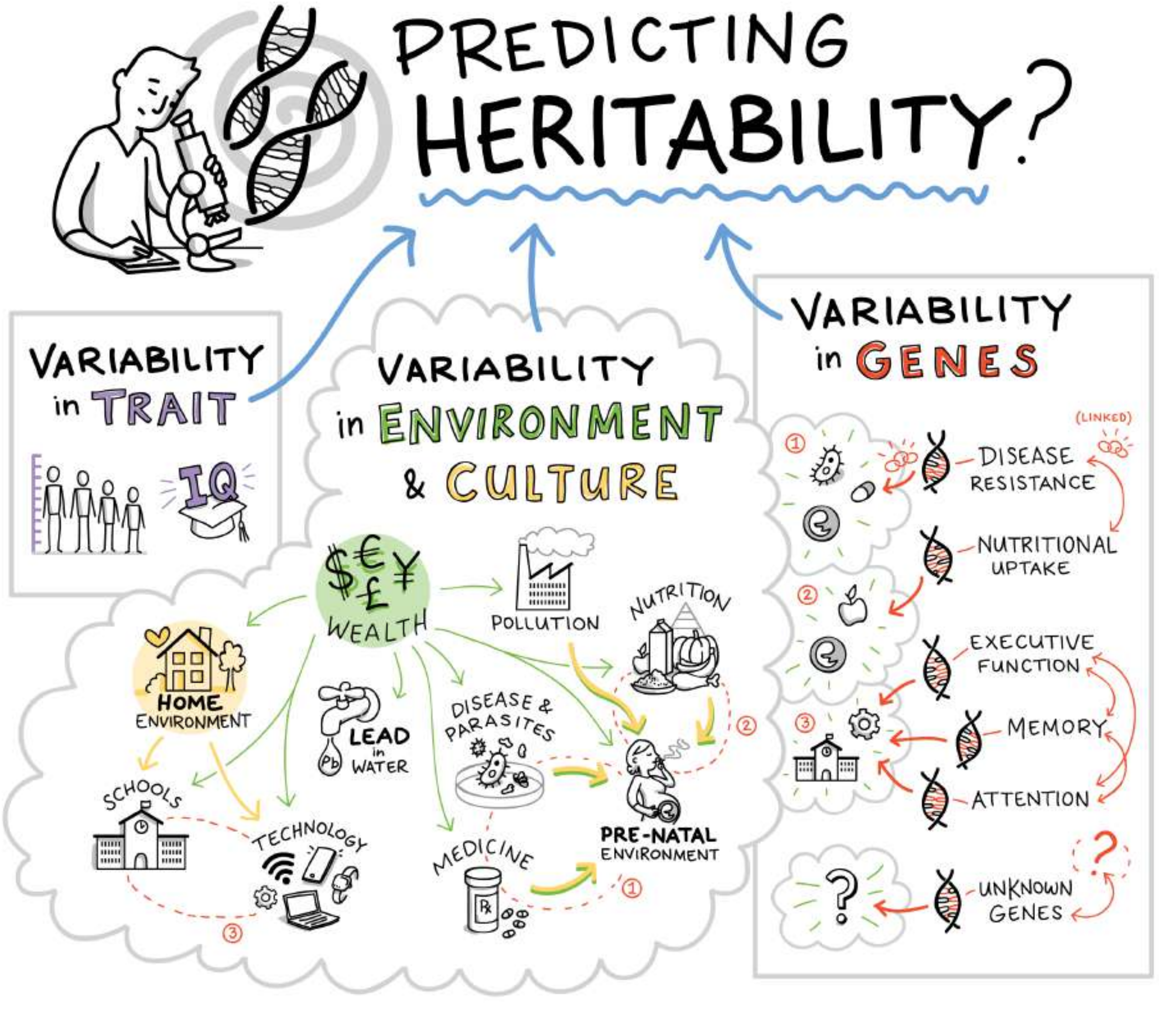

Figure 3.2: Genetic heritability is a function of variability in the phenotypic trait, variability in the environment, including the cultural environment, and variability in genes. Although heritability is often interpreted as a genetic effect, cultural evolution and diffusion can also systematically shape the variability of environmental variables, and thus heritability. Psychological and behavioral phenotypes are typically the outcome of a complex network of interactions that involve all these factors.

Cultural evolution shapes heritability

Assume that for a given society we were able to collect comprehensive data on genetic effects across all relevant environmental variables that contribute to some trait. This would allow us to exhaustively map out the reaction norms (pattern of phenotypic expression across a range of environments) that specify expected phenotypic outcomes over the full range of extant genetic and environmental variation, thus setting up the conditions for a G×E analysis. But in a species like ours, extant environments are not necessarily a meaningful backdrop against which to judge genetic effects. Human environments have already been shaped over deep historical timescales by cumulative cultural evolution—functionally overlapping with genetic evolution (Richerson, Boyd, and Henrich 2010) and can therefore obscure our interpretation of genetic evolution, unless properly accounted for. For humans, the environmental axes of a reaction norm analysis do not simply map out the space of environmental parameters that impact phenotypic outcomes; they rather map out the local and global peaks that have already been climbed by cultural evolution, which correspond to the many solutions to problems that have been discovered and refined over human history. Because cultural evolution enables faster adaptation than genetic evolution, a substantial portion of our adaptations are built into our cultures rather than our genomes.

The human environment is deeply shaped by culture. As heritability is a function of both genetic and environmental variance, cultural evolution carries significant implications for the interpretation of heritability. This idea goes back to the beginnings of the cultural evolutionary paradigm. For example, two founders of the field of cultural evolution, Cavalli-Sforza and Feldman (1973), modeled the effect of parent-to-child ("vertical") cultural transmission on standard behavioral genetic estimates of genetic effects, showing that vertical transmission should inflate heritability estimates relative to a gene-only model. In contrast, here we focus on a different aspect of the interplay between culture and heritability, namely how oblique and horizontal transmission can impact heritability through processes of broad diffusion across a society that systematically shape phenotypic distributions. We begin this discussion by describing the effects of cultural diffusion and innovation upon heritability, as well as the predictions we can make for differences in heritability between societies.

Cultural diffusion

In human societies, mechanisms such as conformist-biased learning (learning from the majority or plurality at a rate above population frequency; Muthukrishna, Morgan, and Henrich 2016; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), payoff biases (e.g. learning from successful others; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), and norm enforcement (identifying norms and punishing norm violators; Chudek and Henrich 2011) result in particular behaviors, beliefs, and norms disseminating widely across a society. To the degree that these cultural traits mask the effects of genes (such as in the skin cancer and vitamin D examples), heritability is reduced. In contrast, to the degree to which these cultural traits unmask or interact positively with genes without masking, heritability is increased.

One example that can illustrate both masking and unmasking through diffusion are genes that support the perception of lexical tone in tonal languages like Cantonese and Yoruba (Dediu & Ladd, 2007; Wong et al., 2020). To the degree that tonal languages like Cantonese or Yoruba diffuse in the population (and holding constant other genetic contributions), heritability of language ability would increase in a manner proportional to variation in these genes; to the degree that non-tonal languages like Norwegian or Russian diffuse in the same population, heritability of language ability would decrease. As another example: it is known that fertility is predicted by genes (Zietsch et al., 2014), but Briley, Harden, and Tucker-Drob (2015) report a large rise in the heritability of fertility in the US over mid-20th century, likely due to the increase in the variety of acceptable reproductive choices that was brought about by the diffusion of new social values. In this case, an increase in cultural variance unmasked the effect of genes associated with reproductive behaviors and preferences. Conversely, cultural or policy changes that reduce variation in reproductive practices—such as rigid childbearing norms or a one-child policy—would be expected to mask the genetic effect.

The diffusion of cultural traits is not random and is in fact well studied within cultural evolution and elsewhere (Rogers 2003; Henrich 2001; Muthukrishna and Henrich 2016). One mechanism for cultural diffusion that is important in industrialized societies is formal education. We use this example, because the effect of this particular cultural institution on heritability has been studied. Samuelsson et al. (2008) measured the heritability of reading and spelling test scores. Australian twins demonstrated a narrow-sense heritability of 0.84 in kindergarten and a similar score of 0.80 in Grade 1. In contrast, Swedish and Norwegian twins demonstrated a heritability of only 0.33 in kindergarten, rising to 0.79 in Grade 1. Heritability was at the same level in both the Australian and Scandinavian children in Grade 1, but not in kindergarten. Why? Cultural diffusion of literacy. Australian children begin receiving compulsory literacy instruction in kindergarten, while in Scandinavia the kindergarten curriculum emphasizes social, emotional, and aesthetic development—literacy instruction only begins in Grade 1. Here we see the effect of national curriculum policy differences affecting cultural diffusion of literacy and thus heritability, in a case where the cultural trait interacts with genes. Australian kindergarteners are exposed to standardized environmental input and much of the remaining variation in reading ability is explained by genetic differences, whereas for the Swedish and Norwegian kindergarteners, variation in the amount of reading instruction received at home is much larger than any genetic differences. In line with this interpretation, Samuelsson et al. (2008) show that the boost in heritability among the Scandinavian children was also accompanied by an almost equivalent decrease in phenotypic variance attributed to the common (home) environment, which would include home instruction.

If we were to assess the genetic basis of literacy skill in schoolchildren without accounting for the impact of their particular educational curricula on cultural diffusion and environmental variation, we would be subjecting ourselves to a selection bias, with no idea of the magnitude of this bias. This would distort our understanding of the generalizability of our finding to samples that have undergone different educational curricula, and even more so to those with different levels of educational attainment. Note that even the literacy instruction provided in the home environment is already shaped by cultural evolution, both in terms of the content being transmitted (reading and spelling), and the structures that are transmitting (family organization in Western countries; Schulz et al. 2019; Henrich 2020). In societies that produce literate children, culture impacts the heritability of literacy from the moment that variation in this trait emerges in development, virtually sealing off the possibility of assessing 'baseline' heritability without cultural interference, even at the very start of life (e.g., children born in literate societies are typically surrounded by writing and literate adults). Heritability is a composite measure that captures both genetic and cultural effects, and without knowledge of the cultural context, it is difficult or impossible to judge what is being measured. When we say that the heritability of reading among Scandinavian children jumps up to 0.79 when they enter Grade 1, this measurement reveals just as much if not more about the disseminative power of modern schooling as it does about the genetic basis of literacy.

Looking toward a broader social context, several insightful studies have shown that the heritability of educational attainment increases with equality of opportunity. We see evidence for this within countries over time (Heath et al., 1985), within and between countries over time (de Zeeuw et al., 2015; Engzell & Tropf, 2019), and within countries following a major policy change (Colodro-Conde et al., 2015; Rimfeld et al., 2018; Ujma et al., 2020). Although there is also some evidence going in the other direction (Silventoinen et al., 2020), the overall pattern appears to be that diffusion of educational opportunity results in genes explaining a relatively greater proportion of variance in educational attainment. These studies serve as robust demonstrations of how heritability can be boosted by changes in social context broadly, and diffusion of particular forms of environmental exposure more specifically. Although these patterns are broadly consistent with our thesis, both the consistent and inconsistent results may obscure cultural structuring, such as the hidden cluster problem and cultural Simpson's paradox, as we discuss below.

Cultural innovation

The human capacity for cumulative cultural evolution (Dean et al., 2014a; Henrich, 2004a) ensures that in our societies, the diffusion of extant cultural traits goes hand-in-hand with the continual generation of new cultural traits. Whether emerging through serendipitous discovery, iterated trial-and-error, or recombination of ideas, some portion of new technologies and behaviors manages to spread across a society, displacing other competing variants. The dynamics of innovation are a significant component of the cultural evolutionary framework (Henrich, 2004a; Muthukrishna & Henrich, 2016a).

Cultural evolution predicts that societies will vary in their rate and type of cultural innovation (e.g. number of patents and incremental vs. revolutionary invention) due to differences in, for example, the size and interconnectedness of their social networks (sociality), effectiveness of cultural transmission (e.g. education), and tolerance for diversity; for review see Muthukrishna and Henrich (2016). Tolerance for diversity can drive differences in heterogeneity. Some societies such as Pakistan and Indonesia maintain relatively low levels of cultural heterogeneity, whereas others such as Brazil and Australia maintain relatively high levels of heterogeneity. One metric that can serve as a proxy for this tolerance is *cultural tightness/looseness*, which represents the degree to which societies tolerate deviation from social norms, and is expected to correspond to their rate of innovation (Gelfand, 2018; Gelfand et al., 2006, 2011b). Societies that are more tolerant of cultural variation allow for more individual-level exploration, and if the best of these cultural mutants can be selectively incorporated into the mainstream, those societies will tend to undergo higher rates of increase in cultural complexity (Henrich, 2004a). Cultural variation is the engine of cultural change. Aside from variables like cultural looseness, policies such as social safety nets and forgiving bankruptcy laws can also create the incentive structure for promoting exploration and innovation (Muthukrishna & Henrich, 2016a).

The initial spread of an innovation will be tied to an increase in environmental variance if that innovation is disrupting an earlier, relatively homogenous state. To the degree that innovation is masking genes, heritability will begin to decrease. To the degree that innovation is unmasking genes, heritability will begin to increase.

Predicting differences in heritability across societies

Over long historical durations, cultural evolution tends toward a compressive environmental effect, as ecological problems are solved and more favorable environmental conditions spread. But on shorter timescales, diffusion and innovation have opposing effects on environmental variance. Although indoor plumbing, antibiotics, and formal education have diffused to the point of being ubiquitous in the Western world, new innovations are also constantly emerging. During their early spread, such innovations increase environmental variance and between-group differences, thereby bringing forth new forms of diversity and inequality. But as these new traits diffuse further, some of them become gradually established within the cultural corpus, reducing environmental variation through homogenization. The dynamics of diffusion and innovation thus differ in their effects, although the magnitude and direction of these effects also depend upon whether the trait in question masks or unmasks genetic variation. Moreover, across societies, the balance between diffusion and innovation differs as well.

If we imagine a society in which innovations are rapidly diffused across the whole society shortly after they emerge, the society will have a low level of cultural variation at most times. This is a society in which a high rate of diffusion quickly overpowers the environmental variance-increasing potential of cultural innovation. Now imagine a contrasting society in which innovations take a much longer time to diffuse. Perhaps the society is more culturally clustered with less interaction between individuals in different subgroups, or perhaps there is a subset of individuals who are well-connected with the inventor and become early adopters but the novel trait diffuses only gradually beyond this inner circle. This would be a culturally unequal society that is characterized by high environmental variability at any given point in time. This kind of stunted diffusion may suggest cultural clustering, with relatively dense connections within subgroups and relatively sparse connections between subgroups. In such societies, even highly useful forms of cultural knowledge may not easily permeate social barriers, and the waves of environmental change are correspondingly 'loose'. These barriers are not necessarily ethnic boundaries: they could be organized around class, wealth, occupation, political alignment, religion, or incidental geographic layout. A society may be clustered for reasons that stem from within the society itself, or it could simply be a matter of nominal mismatch between the political boundaries that we use to refer to a society and the actual organization of cultural groups. Greater differential clustering can lead to a cultural Simpson's paradox (discussed below).

We can derive testable hypotheses from these dynamics: culturally homogeneous societies will have higher heritability for culturally transmissible phenotypic traits[15] compared to culturally diverse or clustered societies. We model this prediction in the Appendix. One way to measure cultural diversity would be to use cultural tightness/looseness as a proxy (Gelfand et al., 2006, 2011b). One way to measure cultural clustering would be to use the cultural fixation index (CF_{ST}) as a measure of cultural distance between groups within a society (Muthukrishna

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[15] Culturally transmissible traits are those whose distribution can be shifted by cultural learning (e.g. many psychological and behavioral traits).

et al., 2020a)—we discuss this in more detail in Section 0. Whatever the measure, homogeneity of cultural traits should be associated with higher heritability on average, but with respect to specific traits, the relationship between homogeneity and heritability will also depend upon the genetic masking or unmasking effect of the trait.

For cultural traits that neither mask nor unmask genetic effects, heritability will generally be higher in culturally homogeneous societies than in culturally diverse societies due to the reduced environmental variance that is a consequence of behavioral uniformity, as described above. For cultural traits that unmask genes, heritability will be higher overall compared to traits that neither mask nor unmask, and on average higher in homogeneous societies than in diverse societies. For cultural traits that mask genes, heritability will be lower overall compared to traits that neither mask nor unmask, but whether it is higher in homogeneous or diverse societies will depend upon which has the stronger effect: genetic masking or the reduction in environmental variance accompanying homogeneity. If the effect of genetic masking is stronger, heritability will be lower in culturally homogeneous societies than in culturally diverse societies; if the reduction in environmental variance is stronger, heritability will be higher in homogeneous societies than in diverse societies.

Thus heritability estimates reflect cultural evolutionary dynamics. Researchers such as Harden (2021) have highlighted how heritability can be used as a tool for measuring useful characteristics across environments such as cross-national differences in social opportunity. These interpretations are consilient with our approach, but are limited by treating the environment as exogenous rather than modeling its dynamics and interactions. Such complexities in the role of the cultural environment have historically been obscured, due in part to a number of methodological and epistemological problems that encumber standard behavioral genetic analysis.

Problems that obscure the effect of culture

The effects of cultural evolution on our understanding of heritability are complex, but we hope that at least the significance of this relationship has now become more obvious. At the very least, we hope this target article will spark a vibrant discussion of the role of cultural evolution in behavioral genetics. There are several features of behavioral genetic methodology that tend to obscure the effect of culture and cultural evolution. Here we will discuss three of these problems—the WEIRD sampling problem, the hidden cluster problem, and the causal locus problem—and then describe a cultural Simpson's paradox that emerges at their junction. Various aspects of these problems have been discussed in prior literature, but we will focus on how the problems specifically interact with the detection and interpretation of effects stemming from cultural evolution. Clarity regarding these issues will be a first step toward integrating the cultural evolutionary framework with behavioral genetics.

WEIRD sampling problem

Behavioral genetics suffers from its own variant of the Western, educated, industrialized, rich, democratic (WEIRD) people problem, which was originally raised in the field of experimental psychology (Apicella et al., 2020; Henrich et al., 2010). The WEIRD people problem refers to the vast over-representation in published studies of individuals from developed Western countries, who are similar in their cultural history, social values, and standards of living. Just as behavioral experimental samples are psychologically WEIRD, behavioral genetic samples are both genetically and culturally WEIRD. This results in a WEIRD sampling problem that limits the variation required to make sense of genetic effects. This problem involves both genetic and cultural restriction of range, and we will discuss each in turn.

WEIRD genetics

A comprehensive meta-analysis that claims to contain essentially all twin studies published between 1958 to 2012 (Polderman et al., 2015a) reveals that 94% of sampled twin pairs were from Western populations. The United States, United Kingdom, and Australia alone accounted for almost 60%, and Nordic countries accounted for another 25%. Of the non-Western countries (6%), two thirds (4%) are from northeast Asia—specifically, China, Japan, South Korea, and Taiwan, countries that are not Western, but have most of the remaining letters of the WEIRD acronym. The remainder of the world, representing the vast majority of the human population, accounts for only 2% of the dataset.

GWAS too suffers from a myopic focus on WEIRD genomes (Need & Goldstein, 2009; Popejoy & Fullerton, 2016; Sirugo et al., 2019). As of 2017, 88% of samples in GWAS were of European ancestry (Mills & Rahal, 2019)[16]. Paralleling the twin studies data, 72% of participants were recruited from just three countries—US, UK and Iceland—with nearly 20% of the remainder being recruited from Japan, China and South Korea.

Polygenic scores do not translate well across ancestry groups (Bitarello & Mathieson, 2020; Curtis, 2018; Guo et al., 2021; Kim et al., 2018; Martin et al., 2017, 2019). For example, European ancestry-derived polygenic scores have only 42% of the effect size in African ancestry samples (Duncan et al., 2019). From a cultural evolutionary perspective, this is not unexpected given the cultural environment, coevolution between culture and genes, and cultural differences between populations.

Polygenic scores are also highly sensitive to inadequately controlled population stratification (Berg et al., 2019; Morris et al., 2020; Sohail et al., 2019). Even within a single ancestry group, the predictive accuracy of polygenic scores can be dependent on age, sex and socio-economic status (Mostafavi et al., 2020)—this too, from a cultural evolutionary perspective, is not unexpected given the cultural variation that exists within a population (Muthukrishna et al., 2020a; Muthukrishna & Henrich, 2019b). Similarly, the SNPs that contribute to the variance of a trait are different in different populations (Akiyama et al., 2019; Gurdasani et al., 2019; Pemberton et al., 2018; Rotimi et al., 2017) and it is difficult to disentangle the genetic, environmental and cultural contribution to differing polygenic scores between populations (N. A. Rosenberg et al., 2019). Recent projects have aimed to capture a greater degree of global human genetic diversity (e.g. Simons Genome Diversity Project, Mallick et al. 2016; the exome analysis of Lek et al. 2016; and the GenomeAsia project, Wall et al. 2019), but we are far from proportionately representing the genetic diversity of the global population.

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[16] An improvement from 2009 when 96% of GWAS participants were of European ancestry (Need & Goldstein, 2009)!

WEIRD culture

When we restrict the scope of genetic samples, the cultural environment against which genetic effects are evaluated also becomes skewed, and this greatly reduces the interpretability of genetic effects. Due to a combination of cultural group dynamics (Chudek and Henrich 2011; Henrich 2004b; Richerson et al. 2016) and cumulative cultural evolution (Dean et al., 2014a; Henrich, 2004a), the human species is characterized by large amounts of cultural and hence environmental variation between societies, which exceeds genetic variation by orders of magnitude (Bell et al., 2009). The WEIRD countries that are over-represented in genetic samples are clustered together along multiple cultural dimensions (Hofstede, 2001; Inglehart & Welzel, 2005; Muthukrishna et al., 2020a), and are perhaps an extreme unrepresentative outlier on many psychological and behavioral measures, with these countries registering the highest scores for traits like individualism, analytical thinking, and prosociality toward strangers, and the lowest scores on opposite constructs such as collectivism, holistic thinking, and prosociality toward relatives but not strangers (Henrich et al., 2010b; Henrich, 2020; Muthukrishna et al., 2020a; J. F. Schulz et al., 2019).

WEIRD societies are also roughly aligned on basic environmental factors like technology, civil infrastructure, healthcare, schooling, and transportation, with typically advanced levels in each of these. Within each of these countries as well, inequality is low compared to non-WEIRD countries, as can be inferred from the comparatively low Gini coefficients of Western countries, with the US being somewhat of an unequal outlier (Selita & Kovas, 2019).

Just as this restricted cultural range limits our understanding of human psychology (Henrich et al., 2010b), it also limits the inferences that can be made about human genetics. Behavioral geneticists understand that genes can have different effects under different environmental conditions (Assary et al., 2018; Moffitt et al., 2005), but there is less appreciation of how those environmental conditions and interactions change through cultural evolution. Cultural evolution can mask or unmask genetic effects, such that gene function becomes confounded with the effect of the cultural environment in a manner that is dependent on the specifics of the underlying dynamics. Cutting through this confound requires a theoretical understanding of the cultural dynamics as well as empirical data on genetic effects across a wide variety of cultural environments. The WEIRD sampling problem therefore harms accurate inference of genetic effects.

Hidden cluster problem

Despite this severe restriction of range among behavioral genetic samples, these samples may also paradoxically be too inclusive. This is due to the presence of cultural clusters that introduce population structure into genetic samples, but which remain hidden to standard behavioral genetic methods. A cultural evolutionary approach can help reveal environmental structure that does not necessarily map onto conventional demographic groupings.

Cultural clustering

Whether the method is a twin study or GWAS, behavioral genetic studies typically draw their data from databases such as twin registries or biobanks, whose coverage spans some circumscribed geographic range such as a country or a subnational region. Because these samples trace over political or administrative boundaries, they may not match up with the actual structure of environmental variation, which will often be dependent upon the organization of cultural clustering. Culture generally tends to agglomerate, such that groups of individuals who are bound together by dense links of cultural influence share a substantially greater number of features of their cultural environment than do individuals who belong to different groups (Richerson et al. 2016). As has been discussed extensively in the cultural evolutionary literature, this in-group similarity is generated and maintained by processes such as conformist learning (Boyd & Richerson, 1985), norm enforcement (Fehr and Fischbacher 2004; Chudek and Henrich 2011), symbolic markers of in-group membership (Boyd & Richerson, 1987), and cultural group selection (Henrich 2004b; Richerson et al. 2016). The structure of environmental variation is thus shaped by networks of cultural interaction, and the topology of these networks is assembled over time by cultural group dynamics and cultural evolution.

A highly clustered population is one that can be easily partitioned into multiple subgroups whose members share among each other cultural traits that are substantially different from those found in other subgroups. When we know the underlying social network, network clustering algorithms (Emmons et al., 2016) can help identify these clusters. When we have measures of a range of cultural traits, we can see the effects of clustered cultural influence by measuring the cultural distance between subgroups, for example by using CF_{ST} (Muthukrishna et al., 2020a). CF_{ST} applies the 'fixation index' (Cavalli-Sforza, Menozzi, and Piazza 1994) to the World Values Survey of cultural beliefs and behaviors (Inglehart et al. 2014), and can quantify the cultural differentiation between any two groups. When applied to sub-groups within societies, this measure can tell us, for example, the degree to which Singaporean Catholics differ from Singaporean Protestants, thus identifying the degree to which a nation state or other political grouping contains large clustering (note that this is different to diversity—a country may be diverse, but uniformly so, showing no large clustering).

Cultural clusters are typically created by barriers that impede cultural interaction, such as topography (e.g., mountain ranges or bodies of water separating populations) or cultural conflict (e.g., conflicting religious beliefs). Mutually unintelligible languages are an example of a social barrier that impedes cultural and even genetic mixing. Thus, the density of languages within a population will also predict clustering. A topographically fractured country like Papua New Guinea with its 839 often mutually unintelligible languages is likely to be a much more clustered population than an equally populated but less multilingual society like Austria. Populations can also become clustered due to more extrinsic factors. Countries that grew through recent immigration, like Canada, are likely to have more clustering than countries that are characterized by relative cultural homogeneity, like Japan (Fearon, 2003). Countries whose borders are drawn arbitrarily with respect to the geographic arrangement of cultural groups, for example as a product of past colonial administration (many countries in Africa), are also likely to have high clustering (Michalopoulos & Papaioannou, 2020). Note the parallel between the present argument and assortative mating (Schwartz, 2013): whereas assortative mating results in phenotypic clustering due to reproduction, cultural transmission results in phenotypic clustering due to segregated learning.

Moreover, cultural clusters may cut through divisions of society that we don't always think of as being 'cultural', such as stratification by social class or wealth. The strength of this stratification regulates the amount of within-stratum versus between-stratum cultural interaction. Although this picture may be complicated by factors such as prestige bias engendering asymmetric influence from upper to lower classes (Henrich & Gil-White, 2001b), such forms of social hierarchy can create clusters. These examples show that cultural clustering is not necessarily bound by geographic contiguity. Although spatial proximity is a good predictor of cultural influence, cultural influence may also be decoupled from geography, particularly with modern forms of mass media and information technology (Martin & Yurukoglu 2017; Anderson 2006). In section 0, we discuss in more detail how cultural clustering may contribute to the phenomenon of differential heritability across socio-economic levels.

In sum, the scope of a genetic sample is often defined by political and administrative boundaries, but these boundaries may be mismatched to the organization of cultural clusters within a society, and the extent of this mismatch will vary greatly across populations. So in addition to measuring cultural variation (diversity) using indices such as cultural looseness, we need to also measure cultural clustering ("segregated diversity") to fully understand the environment. Once we are able to do this, the next intellectual step would be to achieve an understanding of the superimposition of cultural and genetic clusters as well as their interaction.

Contrasts between cultural and genetic clustering

Behavioral geneticists have devoted much effort to the study of genotypic clustering, usually referred to as population stratification or population structure. Populations can become stratified in the presence of genetic variation arising from systematic differences in subpopulation ancestry or from other forms of structured, non-random mating (Brumpton et al., 2020). This kind of genetic clustering can introduce spurious associations between genotypes and traits. As such, researchers continue to develop an array of methods for dealing with this problem (Hellwege et al., 2017; A. L. Price et al., 2010).

Genetic clustering and cultural clustering are linked—a well-known example is the close alignment of genes and languages in historical populations (Cavalli-Sforza, 2001; Cavalli-Sforza et al., 1988; Pagani et al., 2012; Tishkoff et al., 2009). This gene–language alignment occurs because languages, like genes, have traditionally been transmitted vertically—that is, from parents to children or within the family. This is due to critical periods for language learning that close as early as 6 months for phonology (Kuhl et al., 1992) and year 7 for grammar (Johnson & Newport, 1989), due to plasticity in the relevant cortical networks being progressively staunched by "molecular brakes" (Werker & Hensch, 2015). Early learning of this kind is primarily dispensed by parents or other immediate caretakers (Hewlett et al., 2011; Kline et al., 2013), and it is unsurprising that genes and languages should be largely aligned in reconstructions of population history[17].

However, beyond early childhood, children become increasingly exposed to other children from different families as well as to non-kin adults, and the range of sources for cultural learning widens accordingly: a two-stage model of cultural learning (Kline et al., 2013). Due to transmission through these horizontal (i.e., age-peers) and oblique (i.e., non-parent adults) channels, cultural learning becomes untethered from strict vertical transmission and extends laterally across genetic lineages, similar in structure to horizontal gene transfer that is prevalent in bacteria and archaea (Soucy et al., 2015). Like horizontal gene transfer, horizontal cultural transmission is rapid, due to it being unconstrained by the generational cycle of vertical transmission. Oblique and horizontal transmission play a large role in cultural diffusion both within and across extant small-scale societies (Henrich & Henrich, 2010; Hewlett et al., 2011; Kline et al., 2013), just as they do in large-scale industrialized societies where innovation, knowledge and practices across domains such as technology, art, education, political systems, and supernatural beliefs commonly diffuse horizontally (Rogers, 2003). Indeed, with only vertical transmission, culturally evolution as it is currently understood would not work (Enquist et al., 2010b). The importance of oblique and horizontal transmission in human cultural evolution may have been amplified by adaptations such as the timing of weaning relative to brain maturation, which is substantially earlier in our species than would be expected on the basis of our close primate relatives, thereby expediting the human child's exposure to cultural models other than parents (Finlay & Uchiyama, 2020; Hawkes & Finlay, 2018).

Due in part to horizontal transmission, the diffusion of culture can occur much more rapidly than the diffusion of genes, or "demic" diffusion. In historical populations, the speed of demic diffusion has been limited by rates of reproduction and migration (Ammerman &

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[17] Note that this is not the case for modern multicultural populations that can expose children to languages not spoken by their parents or family during this critical period.

Cavalli-Sforza, 1984; Fort, 2012). Horizontal transmission is the diffusion of ideas rather than people and has no such limits; cultural clusters are therefore more fluid and malleable than genetic clusters. For example, if archaeological data show cultural commonality between two contemporaneous populations but genomic analyses suggest disjunction, we can often infer that the shared cultural traits between the two groups were due to cultural transmission rather than migration or admixture (e.g., Olalde et al. 2018; Fu et al. 2016).

Cultural clusters are not only more fluid than genetic clusters, they also explain intergroup differences better than genes do. Cultural distances between neighboring countries are an order of magnitude larger than genetic distances (Bell et al., 2009). Among small-scale societies in Kenya, pastoral clans are differentiated by cultural traits considerably more than they are by genes, and cooperation among these clans is predicted by their cultural—but not geographic—distance to each other (Handley & Mathew, 2020). These findings are consistent with the predictions of *cultural-group selection* (Henrich, 2004b; Richerson et al., 2016), particularly in how competition between cultural trait-groups helps explain the evolution of human cooperation (Henrich & Muthukrishna, 2021). Cultural-group selection requires large differences between groups of cultural traits relative to differences within groups (Apicella et al., 2012; Fehr & Fischbacher, 2003).

Reconciliation between cultural evolution and behavioral genetics requires an update in the way we think about culture. An ethnolinguistic conception of culture that revolves around vertical transmission roughly in alignment with genes is insufficient. For example, linguistic, ethnic, religious, or caste boundaries can create genetic population structure through endogamous marriage practices, whereby individuals marry others who are culturally similar. In the modern world, such assortative mating may be exaggerated as people become more mobile and better connected, making it easier to mate with partners who share cultural traits across many dimensions. Efficiency of assortment may be boosted by cultural matching through dating apps, stretching the tails of the genetic distribution. These are all examples of human culture but they represent only one particular aspect of it, namely cultural effects that channel mating and thereby regulate genetic clusters. This aspect of culture is what appears as signal in population genetic data and is thus often the focus of attention for geneticists insofar as culture is concerned. This ethnolinguistic conception of culture that reduces culture to its effects on genetic clustering is inadequate for comparing genetic effects to environmental effects, given the many non-reproductive cultural effects that shape human phenotypes and environments. Indeed, an understanding of cultural clustering may elucidate novel aspects of genetic population stratification.

Abdellaoui and colleagues (Abdellaoui et al., 2019, 2021) offer evidence for geographic clustering of polygenic scores in the United Kingdom that is statistically independent of genetic ancestry, and explained instead by recent migration. For example, coal mining regions experienced "brain drain" and other forms of trait-conditional departure due to changes in the UK economy over the 20th century. The outcome is detectable in genetic assortment at both the source and destination regions. This is an example of gene–environment correlation, where the environmental factor is a macroeconomic variable with a relatively clear geographic distribution. But this kind of genetic sorting is likely to occur also with respect to environmental factors that are shaped by cultural transmission yet not as readily localizable along geography or other conventional social scientific dimensions. Just as we can use genomic methods to reconstruct aspects of cultural history (e.g., Peter, Petkova, and Novembre 2020; Petkova, Novembre, and Stephens 2016; Dai et al. 2020), a research strategy that builds upon cultural transmission may help us reconstruct and even predict the emergence of genetic clusters that coalesce around—and perhaps feed back onto—cultural clustering of human behavior, psychology, and environments.

Causal locus problem

The hidden cluster problem described the implicit complexity that exists within social groupings, which can hinder robust inference unless parsed properly. Below, we discuss the cultural locus problem, which refers to a source of complexity that exists within the space of functional organization in which genes and culture interact. Inference is hindered here when we view culture as an unstructured exogenous variable, when in fact it is a constructive system that accumulates functional adaptations in a directed manner over time.

Genes that break and genes that make

The more complex a system, the more ways it can fail. Take the history of lighting: compared to the two ways in which a wood-fueled fire can be extinguished (smothering and exhaustion of fuel), there are 7 known failure modes for a fluorescent bulb and more than 30 for the newer LED bulb (de Groot et al., 2013). A faulty rubber O-ring caused the space shuttle Challenger to explode, and a severed fiber-optic cable knocked out internet access for a large swath of people across India and the Middle East. There is a fundamental asymmetry between the identification of elements that support a system and those that undermine it. A well-functioning system is the product of a design process that has solved many problems and closed many paths that do not work. For such a system, 'something going wrong' can be caused by singular aberrations, but 'going right' or 'going well' are properties of the integrated system as a whole. The notions of success and failure in this context therefore point to very different things. For complex functional systems such as machines and organisms, it is easier to identify ways to break the system than ways to explain or improve it.

Gene function can be viewed through this lens. Organisms are the outcomes of complex, emergent interactions involving many genes and their surroundings (Davies 2014), but there are many ways these interactions can go wrong. It is easier to identify deleterious genetic mutations than beneficial mutations, as deleterious mutations are more common. The space of failure is larger than the space of success, making genes that break more detectable than genes that make. For example, a single mutation can cause Mendelian disorders such as cystic fibrosis and Huntington's disease, but no single mutation creates genius. Over 1000 genes have been linked to intelligence (Davies et al., 2018; Lee et al., 2018; Savage et al., 2018). Each gene only explains a miniscule fraction of variation in intelligence, and the causal mechanisms are unlikely to be straightforward (G. Gottlieb, 2003; Turkheimer, 2000). In contrast to these genes that make, the causal mechanisms behind single gene mutations that cause intellectual disability—e.g. *BCL11A* (Dias et al. 2016), *PHF8* (Bathelt et al., 2016), *ZDHHC9* (Schirwani et al., 2018)—are relatively well understood.

This spectrum of localizability ranging from Mendelian to polygenic to "omnigenic" traits (Boyle et al., 2017) has been discussed extensively, but its interaction with cumulative culture has not sufficiently been appreciated. We have known for a long time that increasing nutrition (Lynn, 1990; Stoch et al., 1982), improving schooling (Ceci 1991; Davis 2014; Ritchie and Tucker-Drob 2018), and removing parasites (Jardim-Botelho et al., 2008) have positive effects on IQ. None of this is surprising, but it means that in a society where parasite infection is kept under control, we would not notice that parasite status correlates with intelligence, due to a lack of sufficient variation in parasite load. For the same reason, a correlation between lead exposure and IQ (Needleman & Gatsonis, 1990; Wasserman et al., 1997) will not be revealed in a society where lead is not a problem. And by corollary, genes that provide protection against malnutrition, parasites, or pollution would only be positively associated with intelligence in environments where these insults occur. In environments where these insults have been removed, the same genes would not be associated with intelligence, and can even be deleterious, as in the well-known example of sickle cell trait (Elguero et al., 2015). Similarly, alleles that protect against parasite infection (Carter, 2013) or lead poisoning (Onalaja & Claudio, 2000) will be predictive of IQ only if the environmental risk factors are present in sufficient quantities.

Cumulative culture masking genes

Our living conditions have not always been the way they are today. Just two hundred years ago, 89% of humanity lived in extreme poverty (Ravallion, 2016), 88% were illiterate (van Zanden et al., 2014), and 43% of children died before they were five years old (Gapminder, 2020). Conditions have rapidly improved: rates of extreme poverty are now 10%, illiteracy is down to 14%, and deaths before five years of age are now 4% (World Bank Group - International Development, Poverty, & Sustainability 2020; UNESCO Institute for Statistics 2013). Of course, even if most are now better off, our world still suffers from immense global inequality. Given this restriction in historical range combined with the WEIRD sampling problem, it is not clear how well the genetic effects that have been catalogued thus far can be generalized beyond the particular cultural and temporal contexts in which they were studied. And even if this generalizability issue is acknowledged in principle, the bounds on generalizability are unknown.

Genes can be functionally masked by cumulative cultural evolution, and we expect that this masking is extensive and systematic. Cultural masking may help explain the limited portability of polygenic scores across populations (Kim et al., 2018; Martin et al., 2017, 2019). There is nothing too mysterious about this phenomenon: it's what happens when there are multiple evolutionary systems operating within a shared space of biological function. To build upon an example discussed by Deacon (2003): vitamin C is an essential nutrient and its acquisition is thereby an essential biological function. Endogenous synthesis of vitamin C requires a gene called *GLO*, and *GLO* is present across most of the animal kingdom. But because vitamin C synthesis is metabolically costly, the gene is inactive in some species that have access to sufficient quantities of the nutrient in their diets (Drouin et al., 2011). These include taxa such as teleost fishes, guinea pigs, many bats, some passerine birds and anthropoid primates, i.e. monkeys and apes (Chatterjee, 1973). Anthropoids for instance occupy a frugivorous niche, and fruits often contain sufficient vitamin C. Here gene function is offloaded onto environmental resources. In turn, this offloading has behavioral implications. If a species becomes dependent on its environment ("auxotrophic") for vitamin C, both its behavioral range and evolutionary trajectory become constrained by the availability of the nutrient. Humans are a nice example of this. As our species migrated across the planet, we found ourselves in environments where vitamin C was in short supply. A deficiency of vitamin C causes scurvy—the bane of seafarers until the trial-and-error discovery that certain food items like sauerkraut and citrus could prevent ships from being packed with tired, bleeding, toothless, and eventually dead sailors (Lamb et al., 2017).

Other species have other ways of obtaining vitamin C from their environments, and once these alternative pathways are established, the function of *GLO* becomes masked. A functionally masked gene is removed from the selection pressures that brought it about in the first place, and can therefore be culled from the genome, as evolution tends to do to unused elements (Albalat & Cañestro, 2016; Wolf & Koonin, 2013). Masking does not necessarily need to be in the direction from culture to genes: we can think of genetic assimilation (Crispo, 2007; Waddington, 1953) as the same process working in the opposite direction, where a trait that is regularly acquired through learning gradually transfers its locus to the genome (see Baldwin effect; Morgan, Suchow, and Griffiths 2020). Genetic assimilation can eliminate the cost of learning, but only by sacrificing flexibility. The masking of genes by cumulative culture can eliminate the metabolic cost of endogenous synthesis in the case of vitamin C, and perhaps other costs in other cases, but only by sacrificing reliability of outcome.

Culture and genes are tightly intertwined in this manner, but this kind of functional interaction occurs across various levels of biological organization: between genes within the same genome—*intragenomic* (Phillips, 2008), between nuclear and organellar (mitochondria and plastid) genomes—*cytonuclear* (Sloan et al., 2018), and between host and microbial symbiont genomes—*holobiontic* (Bordenstein et al., 2015). Mitochondria, for example, are believed to have undergone extensive reductive evolution, transferring nearly all of their genes to the nuclear genome (Sloan et al., 2018; Wolf & Koonin, 2013). Indeed, the residual mitochondrial and nuclear genomes collaboratively assemble "chimeric" proteins (Osada & Akashi, 2012). This kind of coevolution is not uncommon in the history of life (Laland et al. 2015; Jablonka and Lamb 2005).

Similar to these cross-level interactions, culture and genes are interwoven in the construction of many behavioral traits, making separation effectively impossible. Because these two systems interact within a shared space of phenotypic variation, a focus on only one or the other leaves significant ambiguity in the causal underpinnings of these phenotypes. For example, is language primarily the result of culture or genes? Such a question can be answered only by recourse to both sides of our dual inheritance (Chater et al., 2009; Christiansen & Chater, 2008; Deacon, 1997; Dediu, 2011; Dediu & Ladd, 2007; Wong et al., 2020). Epistemological biases in the interpretation of the causal loci of phenotypic traits can misinform policy decisions and impede progress in the research and development of beneficial interventions. Given the inherent ambiguity that arises because of gene–culture interaction, it is important to adopt a sufficiently integrative framework to interpret findings.

Cultural Simpson's Paradox

The WEIRD sampling problem, the hidden cluster problem, and the causal locus problem are fairly general issues. But when we consider them jointly, the three problems contribute to a more specific problem that is perhaps not so obvious without a cultural evolutionary perspective. In particular: cultural adaptations that mask genetic effects (causal locus problem) can confound the measurement of genetic effects when the researcher lacks information about the fine-grained distribution of cultural adaptations (hidden cluster problem) and simultaneously lacks access to a sufficiently broad range of samples that could otherwise cut through the cultural confound (WEIRD sampling problem). This set of problems can create a Simpson's paradox (Kievit et al., 2013; Simpson, 1951): the association between two variables qualitatively changing after controlling for subgroup structuring.

As an example, consider UV once again. In section 0, we discussed how mismatch between genes (skin pigmentation) and ecology (UV levels) can be masked by the cultural diffusion of sunscreen, especially in regions with more exposure to sunlight. In other parts of the world, the more important health issue is the set of problems associated with under-exposure to the sun, which causes vitamin D deficiency. Low vitamin D is associated with a broad range of risk factors, most significantly for bone integrity but also for muscle strength, autoimmune disease, cardiovascular disease, cancer (Holick, 2007), and perhaps COVID-19 (Meltzer et al., 2020; Rhodes et al., 2020). Controlling for skin pigmentation, vitamin D deficiency is correlated with latitude: one US study compared a sample in Erie, Pennsylvania (42° N) to one in Bradenton, Florida (27° N) that was matched along many key variables, and found that the northern group had lower levels of serum vitamin D and were at much greater risk of vitamin D deficiency than the southern group (Leary et al., 2017). A study in France similarly found that people in more northern regions had lower levels of vitamin D and a much higher prevalence of vitamin D deficiency compared to people in more southern regions (Chapuy et al., 1997).

Despite this intuitive pattern within countries, several studies have shown that when we compare across countries within Europe, we see the opposite pattern where people in northern countries have *higher* levels of serum vitamin D than people in southern countries (Lips, 2001; Lips et al., 2001; Van der Wielen et al., 1995). This is the case even when data collection is conducted during the winter months when sunlight is scarce, and even when the data are processed by a central laboratory facility, avoiding confounding by variation in laboratory procedures. What's going on? This inverted pattern may be partly due to genetic factors, e.g., people in southern European countries having more pigmented skin, but a substantial part of it is likely due to culture. As an explanation, various researchers have pointed to the high consumption of fatty fish and cod liver oil in Northern Europe, as well as greater sun-seeking behavior in these countries compared to Mediterranean Europe; policies for vitamin D fortification of foods may also give the northern countries an advantage (Brustad et al., 2004; Lips, 2007; Mithal et al., 2009; Pilz et al., 2018). These are potent cultural adaptations: Brustad et al. (2004) fed participants the traditional northern Norwegian fish dish *mølje* three times over a span of two days, and discovered that it had supplied 54 times the recommended daily dosage of vitamin D. Therefore, the relationship between latitude and vitamin D levels goes one way within a country, and the other way between the countries of Europe.

Another example of a cultural Simpson's paradox from Europe is excess mortality in winter months compared to non-winter months across countries: excess winter mortality is highest in warmer countries like Portugal and Malta, and lowest in colder countries like Finland and Iceland (Fowler et al., 2015; Healy, 2003; McKee, 1989). Portugal has the highest excess winter mortality among the countries estimated by Healy (2003) at 28% while Finland has the lowest at 10%, despite a much sharper temperature differential between summer and winter months (as well as lower absolute temperature) in Helsinki and Tampere compared to Lisbon and Porto. This has been called the "paradox of excess winter mortality" (Healy, 2003). The likely cause is that houses in warmer climate regions tend to be poorly insulated, which causes lower indoor temperatures. Populations in these regions also do not wear appropriate clothing when outdoors in cold weather (Healy, 2003; The Eurowinter Group, 1997). In south Finland 72% of people wore hats whilst outdoors at 7°C, but only 13% of people in Athens did (The Eurowinter Group, 1997). A number of studies show that *within* countries, regions with colder winters experience higher excess winter mortality (Aylin et al., 2001; Davie et al., 2007): here too there appears to be an inversion when comparing the effect between countries and within countries.

If we had been Martian anthropologists who did not know that the populated landmass known as "Europe" can in fact be broken down into sub-units called "countries", these examples would be standard examples of a Simpson's paradox (Kievit et al., 2013; Simpson, 1951). In these cases, the paradox occurs when we do not know how to partition the higher-order population (Europe) into lower-order units. Fortunately, we do know how to partition continents into countries, but in other cases, the relevant units may not always be as easily identifiable as countries or administrative regions.

Countries are territorially exclusive political entities, but we can also see them as cultural groups—clusters of cultural traits that can be identified using tools such as CF_{ST}. People within a cultural group share more cultural traits than do people between separate cultural groups. All else being equal, there is more mutual cultural influence among individuals within a country than there is among people between countries. Even when we take a powerful social organizing force like religion into account, co-residents of a country who belong to different religions are more psychologically similar to each other than to co-religionists who live in different countries, although religion nonetheless also explains a sizable amount of similarity (White et al., 2020). This suggests that ideas and practices spread more easily within countries than between countries, and that countries constitute cultural clusters that can be used to partition higher-order levels of organization, such as continents. Countries too may in turn be decomposed into relevant cultural clusters—more acutely in places like Africa, where colonial borders were often drawn arbitrarily without respect for ethnolinguistic groups (Michalopoulos & Papaioannou, 2020), but clustering is prevalent across many countries as revealed by subnational CF_{ST} analyses (Muthukrishna et al., 2020a). To avoid a cultural Simpson's paradox, we must be able to measure cultural clustering.

Hidden clustering creates inferential problems for behavioral genetics precisely because cultural clusters are the most salient unit of organization upon which cultural group dynamics and cultural evolution act (Handley & Mathew, 2020). Cultural evolution is fast and potent but bound within cultural clusters to varying degrees. Because different clusters are each independently able to incorporate cultural adaptations, genetic effects can get differentially masked in a cluster-wise fashion. The extent of this masking varies across clusters, and those that are exposed to greater ecological challenges (e.g., higher latitudes) may build up stronger cultural adaptations and undergo deeper masking. When these cultural adaptations not only compensate for the ecological challenge but overcompensate, and do so proportionally to the magnitude of the ecological challenge, the outcome is an inversion of the natural relationship between ecologies and phenotypes—as we saw above in the inverted correlation between latitude and vitamin D (Brustad et al., 2004; Lips, 2007; Mithal et al., 2009; Pilz et al., 2018) and between latitude and winter mortality (Fowler et al., 2015; Healy, 2003). The cultural Simpson's paradox thus arises when cluster-wise cultural adaptation across an ecological gradient changes the slope of the ecological effect: attenuating, neutralizing, or inverting its directionality depending on the strength of the cultural adaptation relative to the ecological challenge.

Therefore, the relationship between genes, ecology, and phenotype will often be qualitatively different for humans than it will be for other animals. We should be careful of inferential errors that may derive from neglecting the cluster-wise cultural evolution of environments. Even if the gradient of cultural adaptation does not go as far as inverting the ecology–phenotype relationship and instead takes a more moderate form, it can nonetheless confound measurement of genetic or ecological effects. If the arrangement of the cultural clusters within a population is unknown, such gradients may be difficult to detect in the first place.

To summarize the problems that we have discussed thus far: the WEIRD sampling problem and the hidden cluster problem each obscure the variance structure of a sample—the former by concealing the range of total variation that exists outside of a restricted (possibly unrepresentative) segment, the latter by concealing the heterogeneity within that segment. The causal locus problem allows for differential masking among the heterogeneous sub-groups, and poses a challenge to interpretation of gene function, for example in the form of a cultural Simpson's paradox. Collectively, these problems have long obscured the effect of culture within behavioral genetics. Cultural evolution can help us understand phenotypic distributions in human societies as well as more accurately represent the structure of our nature and nurture.

Behavioral genetic puzzles in light of cultural evolution

A dual inheritance and cultural evolutionary theoretical framework can help make sense of various puzzles in behavioral genetics. Here we discuss three: differences in heritability across socioeconomic levels, differences in heritability across development, and the Flynn effect.

Heritability across socioeconomic levels

The heritability of IQ is higher among affluent, high socioeconomic status (SES) households than among poorer, low-SES households in some societies (sometimes referred to as the Scarr-Rowe effect; Scarr-Salapatek 1971; Rowe, Jacobson, and Van den Oord 1999), but the relationship between SES and heritability is mixed in other societies (Nisbett et al. 2012; Hanscombe et al. 2012; van der Sluis et al. 2008; Turkheimer et al. 2003; Giangrande et al. 2019; Platt et al. 2019). A cultural evolutionary perspective can shed light on these findings.

Discrepancies in cultural transmission across societies

A meta-analysis (Tucker-Drob & Bates, 2016) found the gene × SES interaction on IQ in a subset of US samples, but not in samples from Europe and Australia. Pooling the US studies, the authors found an effect size that corresponds to a heritability estimate of 0.61 at 2 standard deviations above the mean SES but only 0.26 at 2 standard deviations below the mean. In western Europe and Australia, heritability is more uniform. The cause of this interaction is still debated.

Several researchers (e.g., Bates, Lewis, and Weiss 2013; Beam et al. 2015; Tucker-Drob, Briley, and Harden 2013) have suggested that gene-environment correlation via phenotype-to-environment transmission, otherwise referred to as 'reciprocal causation', is the most likely explanation. By this explanation, those with genes well suited to a task can better nurture their skills in a wealthier environment than in a poorer environment. That is, initially small differences in genetic potential become gradually amplified over time due to the iterative matching of environments to abilities: an increase in expressed ability brings forth new environmental conditions that enable further growth along that dimension (Bronfenbrenner & Ceci, 1994b; Dickens & Flynn, 2001; Scarr, 1992). Such processes can increase genetic heritability, but through reciprocal shaping between genetic potential and environment, rather than through innately specified ability levels. The reasoning is that high-SES households are able to provide environments that do this more effectively and are thereby able to let genetic potential be more reliably associated with corresponding outcomes, lifting heritability as a result. While such reciprocal causation may indeed be occurring, reconciling this explanation with the findings from Europe and Australia seems more challenging or at least incomplete.

Heritability is a function of the variability in culture, which is shaped by cultural group dynamics and cultural evolutionary forces. In the United States, the differences between, for example, school and home environments among high-SES households are likely to be small relative to differences between school and home environments among low-SES households, where factors such as school lotteries can dramatically affect the cultural input. In contrast, the cultural environment is less unequal in western Europe and Australia, where, for example, high quality schools are available across SES. Where these two explanations make different predictions is for poorer countries. The reciprocal causation explanation would predict low heritability in poorer countries. The cultural evolution of genetic heritability explanation would instead predict high heritability where there is equal access to similarly poor schools and household conditions, but low heritability if inequality is high.

Although environmental variability is commonly construed through the framework of economic inequality, we can also look at it through the lens of cultural variability. For example, even if a society maintains economic equality, it may still contain cultural sub-divisions that lead to multiple clusters each with different traditions and behaviors. When this cultural clustering creates differences in the level of some given trait between clusters, the heritability of this trait decreases in accordance with the strength of the clustering.

We predict that networks of cultural transmission are more fractured (i.e., contain a higher density of cultural clusters) in low-SES households than they are in high-SES households comparing within a country, at least for (but not limited to) transmission of cultural information and influence that impacts traits in domains like cognitive ability. We also predict that these cultural networks are more fractured in the US than in Australia and Europe, with the greatest fracturing expected in low-SES US communities. Moreover, we predict that these differences across groups will explain at least some portion of the interaction between SES and heritability in the measurement of IQ. These effects could be tested through causal identification techniques, including randomized controlled trials or natural experiments such as school lotteries.

A number of studies have examined unstandardized variance components to make sense of the forces that are driving the gene × SES interaction effects for cognitive ability, but the results have been mixed. In some studies, the interaction is apparently due to an increase in variance explained by the shared environment (the C component of the ACE model) in lower-SES households compared to higher-SES households (e.g., Hanscombe et al. 2012; Kremen et al. 2005), while other studies suggest that it is instead due to a decrease in variance explained additively by genes (the A component of the ACE model) (e.g., Bates, Lewis, and Weiss 2013; Kirkpatrick, McGue, and Iacono 2015). The shared environment explanation is more consistent with cultural dynamics, although reality may be more complicated with other processes such as reciprocal causation (Bronfenbrenner & Ceci, 1994b; Dickens & Flynn, 2001; Scarr, 1992) contributing to the same effect through other pathways, such as via moderation of the additive genetic component. Moreover, we would predict that this environmental variance would be reduced if cultural opportunities and transmission networks among low-SES households became more broadly connected, supporting greater cultural homogeneity. This would be true, even if the level of poverty or other indicators of well-being remained just as low. That is, this effect is not about poverty or deprivation per se—heritability can be high even among lower-SES groups—but more about cultural clustering. Simply moving neighborhoods can vastly improve life outcomes for low-SES Americans (Chetty & Hendren, 2018b, 2018a), but we would not predict such large effects for high-SES Americans.

In general, we predict that Scarr-Rowe-like discrepancies in the heritability of IQ will be found when comparing groupings that vary in their degree of within-group cultural clustering (or homogeneity) whenever this clustering imposes barriers upon the cultural transmission of cognitive ability. The more clustered society will be associated with a lower heritability for the trait; this effect would be expected across many culturally transmissible traits beyond IQ as well. When disaggregated by cultural cluster (e.g., SES), we should expect lower heritability among the more culturally diverse and/or more culturally clustered subgroup.

Discrepancies in environmental variation between humans and other animals

Comparing these SES effects in humans with similar experiments in rodents offers additional insight. Sauce et al. (2018) found that mice reared in an enriched environment exhibited lower heritability of a rodent analog of general intelligence (for standard rodent learning tasks such as odor discrimination and navigation) than did mice reared in a control environment, with a heritability of 0.15 in the enriched group versus 0.55 in the controls. The directionality of this difference is opposite of what we have described above for the human literature, and the opposite of what the reciprocal causation explanation would suggest (Bronfenbrenner & Ceci, 1994b; Dickens & Flynn, 2001; Scarr, 1992). If we assume that this type of environmental enrichment paradigm can be mapped onto differences between high- and low-SES environments in humans, as has been argued (Hackman et al., 2010; Rosenzweig & Bennett, 1996), the reported discrepancy between rodent and human studies might appear surprising.

Non-genetic phenotypic variation in mice appears to be generated in part by initially small, random differences in experience being amplified over the course of development (Kempermann, 2019)—complex environments enable greater amplification of these initial differences and hence 'individualization', whether the environmental complexity is of a physical (Freund et al., 2013) or social nature (Shemesh et al., 2013). In these studies, both genes (due to inbreeding) and the shared environment are controlled. It is therefore the non-shared environment, or individually unique forms of experience, that is driving this differentiation. The enriched environment enables a greater range of variation in experience and as a consequence, genetic effects are proportionally reduced.

Compare this to humans, where cultural transmission gradually homogenizes the environment within a cultural cluster (though not necessarily between cultural clusters), and to varying degrees across clusters as well. We predict that high-SES US households as well as households within Australia and European countries are less culturally fragmented than low-SES US households, leading to higher environmental similarity within Australians, Europeans, and high-SES Americans respectively (but not necessarily high similarity between the groups). In other words, relatively enriched environments (high-SES or Australia/Europe) are also those that are more culturally homogenous. This in turn may explain why enriched environments would be negatively associated with heritability in mice (Sauce et al., 2018) but positively associated with heritability in humans at least under certain conditions (Tucker-Drob & Bates, 2016). Our prediction is that the opposite effect between the two species arises because in humans, the amplification of initial differences in experience by complex environments (individualization) is overwhelmed by the homogenizing effect of cultural learning and group dynamics (for example, through oblique transmission from favored models in the previous generation and horizontal transmission from peers). The more variation is generated by enriched environments and individualization, the more incentive there is to learn from successful individuals or from those who are likely to have learned from successful individuals themselves. Cultural diffusion systematically squashes the variation created by innovation (see Appendix for a model of such dynamics).

A cultural evolutionary approach to heritability distinguishes between humans and other animals in ways that a standard behavioral genetics approach does not. Whereas behavioral genetics provides no clear reason to differentiate analysis of genetic effects in humans from genetic effects in non-human animals, cultural evolutionary theory explicitly formalizes the difference between humans and other animals: our extensive dual inheritance (Boyd & Richerson, 1985). The human-specific predictions that arise from a cultural evolutionary behavioral genetics offer clear tests for our hypotheses. The approach may thus also be validated by comparative behavioral genetic analyses between humans and non-human animals. This research direction may help make sense of some of the limitations of non-human animal models, in cases where cultural adaptations create unexpected gaps in generalizability despite sufficient phylogenetic conservation of relevant phenotypes.

Heritability across development

Cultural heterogeneity may also vary across development. Because culture typically acts as a phenotypic homogenizer within cultural clusters, we should be able to detect the influence of culture across development in the form of changes in genetic heritability. How we learn and who we learn from changes over the lifespan. One especially important transition is the shift from learning primarily from parents and other family members to learning from more distant models who are selected from a broader swath of society (Cavalli-Sforza and Feldman 1981). In the first of these two phases, there is less choice in what to learn, and much of the acquired knowledge is passed down through the same route as genetic information—from parent to child—by *vertical transmission*. In the second phase, the child is more independent, and has the opportunity to update what they have learned from a broader range of models, using learning strategies to decide whom to learn from, by *oblique transmission*. This expansion in learning models is essential for cumulative cultural evolution (Enquist et al., 2010a), and may be facilitated by adaptations such as early weaning (Finlay & Uchiyama, 2020; Hawkes & Finlay, 2018). Building on Cavalli-Sforza and Feldman (1973), who show that vertical transmission inflates heritability estimates by increasing similarity between caretakers and children, our argument focuses on how broad, community-level oblique and horizontal transmission can either inflate or deflate heritability by unmasking or masking genetic effects. Both processes are likely to be operating simultaneously, although if oblique transmission is broad enough, it may weaken the confounding effect of vertical transmission.

This transition from vertical to oblique learning moves the child from the idiosyncrasies of their parents and household to the larger environment they now have in common with other adolescents and young adults. When the child is primarily relying on vertical transmission, the characteristics of their household play a larger role in explaining variation in cultural input, in which case we should expect a high proportion of phenotypic variance to be explained by the shared (home) environment in twin studies. When the child switches to oblique learning, they now share more common influences with other children. Insofar as these traits unmask genetic differences, this would be expected to reduce environmental variation across the population and increase heritability.

This reasoning implies that for phenotypic traits that are molded in real-time by the current shared environment instead of by the persisting effects of earlier parental influence, heritability should increase at this later life stage. Indeed, this is precisely what Hatemi et al. (2009) find in the case of political orientation, or where one lies on a progressive–conservative spectrum, measured in a US sample by questionnaire (Figure 3). Monozygotic (MZ) and dizygotic (DZ) twin pairs are both equally similar from middle childhood up to early adulthood, although the degree of twin similarity increases over time for both. Right around the age at which American children leave home, this pattern is broken, and the phenotypic correlations drop precipitously in DZ twins while remaining steady in MZ twins, and this discrepancy persists for the rest of the lifespan. The drop in DZ but not MZ correlation at this age suggests that the shared home environment exerts a convergent influence for both twin types early in life, but that once this influence is removed, genetic effects become unmasked and able to guide political attitudes independently from the shared environment. More phenotypic variance is explained by genes from this point onward, thus boosting heritability. In countries like Italy and Croatia, where the mean age of leaving the parental household is past 30 (European Statistical Office, 2020), we would predict the developmental time course of heritability to reflect this later independence relative to American samples. Note that the present example has the same overall structure as the literacy example discussed earlier (Samuelsson et al., 2008), with heritability increasing as cultural influences from outside of the home environment kick in. Both examples indicate that heritability can be an index of shared life history and communal structure.

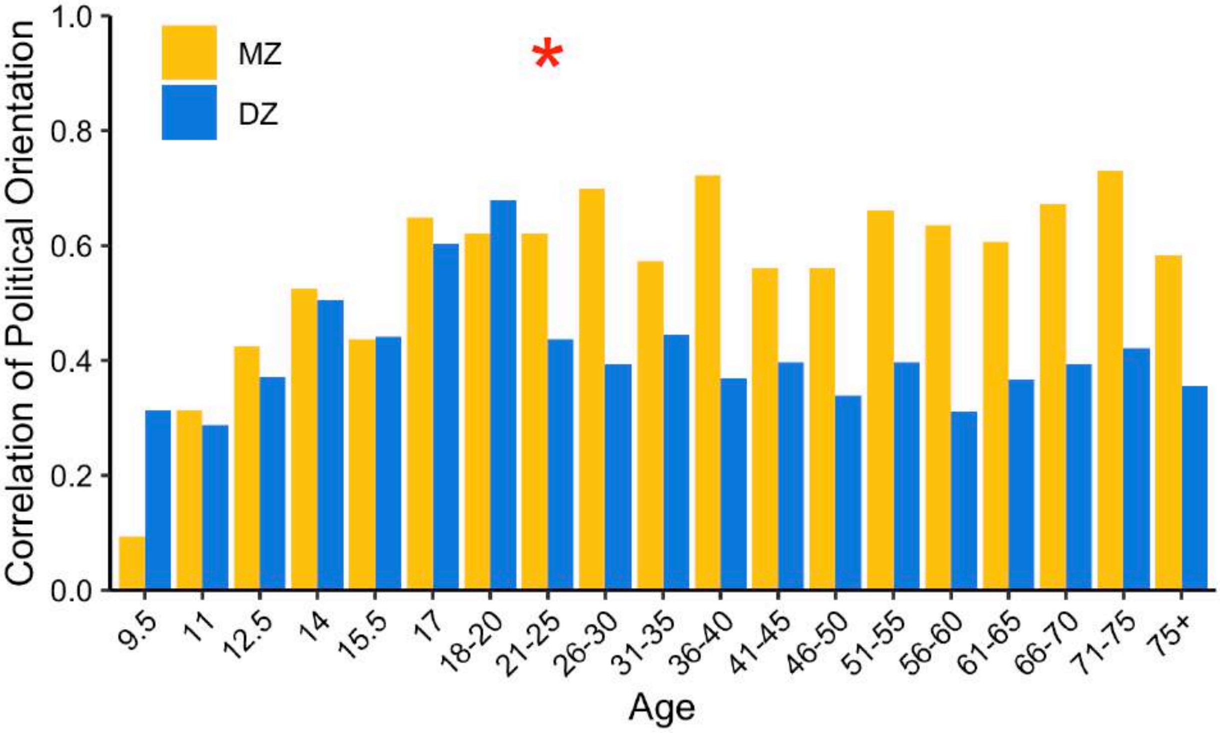

Figure 3.3: Twin concordances in political orientation. In middle to late childhood, within-twin correlations for reported political orientation are roughly the same between Monozygotic (MZ) and dizygotic (DZ) twin pairs in a US sample. In the early 20s, shortly after many US youth leave home for the first time to attend university, the correlation drops for the DZ twins but not for the MZ twins (identified with red asterisk). This shift corresponds to a sudden rise in heritability, as genetic similarity now predicts similarity in political orientation. When the effect of the home environment is weakened and replaced with more diverse cultural input, the effect of genes

becomes unmasked and separates the phenotypic concordances between the two twin types. Horizontal axis indicates age, vertical axis indicates percentage twin concordances in political orientation. Figure reproduced from Hatemi et al. (2009).

Although the use of shared household environment to analyze twin data is a standard methodological convention, the household is in fact just one among many groupings of cultural organization that generate environmental convergence (Harris, 1995b). Households may be the most potent cultural grouping for some phenotypic traits, but other groupings may have significant impact as well for specific kinds of traits. These may include schools, peer-groups, sports teams, religious communities; society-wide groupings such as different mass media and popular culture; more diffuse groupings that are organized around particular sets of values such as political ideology or professional values; and possibly new kinds of groupings such as online communities.

Separating out the effect of household from the effect of genes is typically considered to be an explanatory goal, but there may be further phenotypic variance that could be meaningfully explained if we were able to match phenotypes to other relevant cultural groupings and therefore to other sources of cultural influence. Twins share 'common environments' across multiple scales of social organization in this manner, but when phenotypic similarity is engendered by cultural groupings that extend beyond the household, the resulting correlations will usually be relegated to the broad category of 'nonshared environment', unless membership for example happens to align with household structure (Plomin et al., 2001; Plomin & Daniels, 1987). Although the nonshared environment is typically discussed as environmental exposure that is specific to the individual, it remains possible that there are multiple layers of communal structure embedded within this variance component.

This point becomes somewhat obvious when we consider systems outside of the European Marriage Pattern (Henrich, 2020), such as the Israeli kibbutzim (Lieblich, 2010), the "walking marriages" of the Mosuo of southwest China (Ji et al., 2013), or the communal child rearing of the Ache of eastern Paraguay or of the Hiwi of Venezuela (Hill & Hurtado, 2009). In such societies, similarity of developmental environments may not be adequately parsed at the unit of the household (Kăĝitçibaşi, 1984). The Western notion that socialization takes place primarily in the household may not apply even to Western societies (Harris, 1995b).

If this is the case, then the strategy of looking for phenotypic correlations within the household that are unexplained by genes may be appropriate for answering questions about the specific influence of the household, but is insufficient for answering questions about nature–nurture more broadly.

One potential way to overcome this limitation is to map out clusters of cultural similarity within a society using a tool like Cultural F_{ST} (Muthukrishna et al., 2020a), explained above, and match this finer-grained population structure with genetic data. If assignment to a cluster explains phenotypic similarity over and above that of the shared household, for instance, such methods could be leveraged to capture a broader picture of the environmental factors that guide phenotypic development. If we were able to track the changing organization of these cultural clusters over time, it would allow us to follow the dynamic trajectory of environmental structure and partition this out from measurements of genetic effects longitudinally. We expect social phenomena like urbanization and demographic change to be associated with change in these cultural clusters over time.

General intelligence is another trait whose heritability is known to change over the course of development (Haworth et al. 2010; Briley and Tucker-Drob 2013; for a number of other traits see Bergen, Gardner, and Kendler 2007). This takes the form of a steady increase from childhood through adolescence all the way to early adulthood, after which it remains more or less steady over the lifespan. Although estimates vary, one meta-analysis (Haworth et al. 2010) put the heritability of general intelligence at 0.41 in childhood and 0.66 in adulthood. Explanations for this pattern typically invoke a combination of (1) gradual activation of relevant genes over the course of brain development and (2) active gene-environment correlation or 'reciprocal causation' (Bouchard 2013; Haworth et al. 2010; Plomin et al. 2016; Tucker-Drob, Briley, and Harden 2013).

In contrast, a cultural evolutionary perspective would attribute the rise in the heritability of IQ to the developmental time course of cultural influence. One clear testable prediction is that in a society with different constraints on the development of cultural learning, as in the above example of political orientation, the developmental trajectory of heritability would also differ. A society that engages with communal childrearing immediately from infancy will impose a different set of developmental constraints (and opportunities) compared to a typical Western society. Even in Western societies, cultural development may look very different from now just a few decades into the future, if information technology continues to transform children's networks of social interaction and influence. A cultural evolutionary explanation can help make sense of the relevant data. For example, we predict that sharp changes in heritability will map onto sharp changes in an individual's cultural environment (e.g., the start of school, university, or military service). These milestones may shift due to policy changes, allowing for causal tests of this hypothesis. If, for example, children start higher education later, then large increases in heritability should also occur later.

Whether or not one agrees with our construal of these particular examples, it is logical that genetic effects for many traits become confounded with communal structure unless the developmental time course of cultural influence is properly accounted for. Cultural evolutionary theory predicts that over the life course, cultural influence begins from a primarily parental setting and progressively expands its scope into the greater community, diversifying the models from which an individual can learn (Fogarty et al., 2019; Muthukrishna, Doebeli, et al., 2018a). Insofar as this occurs, we predict a general increase in heritability over the lifespan for culturally malleable traits. The slope of this increase would depend upon cultural parameters and vary by society. Conversely, if there is a correlation between communal structure and the heritability of some trait, this may serve as an index of the cultural malleability of that trait. Our goal here is to bring attention to the conceptual and analytic power that cultural evolution can contribute to developmental behavioral genetics.

The Flynn effect

The Flynn effect describes the rise in IQ test scores over time (Flynn, 1984, 1987)—roughly 2 to 3 IQ points per decade on average around the world (Flynn, 2009; Pietschnig & Voracek, 2015; L. Trahan et al., 2014). The rate of increase differs between countries, being largest in countries that have recently started modernizing, and smallest in countries that had attained modernization by the beginning of the 20th century (for review, see Nisbett et al. 2012). In some countries in Northern and Western Europe including Denmark, the Netherlands, and the United Kingdom, there is evidence that the Flynn effect has been slowing down and even reversing in recent decades (Dutton et al., 2016). This negative Flynn effect is even less well understood than the positive Flynn effect. Bratsberg and Rogeberg (2018) find that in Norway, the negative Flynn Effect is found within families (between siblings), thereby making it unlikely to be explained by demographic changes or immigration, and instead supporting an environmental explanation.

There is no consensus regarding the cause of the Flynn effect, but given the recent and rapid increase, genetic explanations are unlikely. Various hypotheses include increases in test familiarity, improvements in education, sophistication of the technological and media environment, better nutrition, decreasing family size, and slowing life history, and increased out-breeding or 'hybrid vigor' (Bratsberg and Rogeberg 2018; Clark, Lawlor-Savage, and Goghari 2016; Nisbett et al. 2012; Pietschnig and Voracek 2015; Trahan et al. 2014; Johnson 2006; Joshi et al. 2015; Woodley 2012).

Flynn (2007) and Greenfield (1998; 2009) suggest that the effect is caused by a rapid worldwide increase of cultural practices, technologies, and environments that promote abstract cognitive processing as opposed to more traditional forms of concrete, pragmatic thinking. Some examples explored by these authors included urbanization, mass media, video games, education style, counterfactual thinking, and white-collar occupations. This account is mostly consistent with a cultural evolutionary explanation, which would suggest that intelligence is not just about hardware—genes, parasites, pathogens, pollution, and nutrition affecting health and brain development, but also software—the increasingly complex cultural package we acquire from our societies (Bloom, 2020; R. Gordon, 2018; Jones, 2020; Mesoudi, 2011). By this account, not only is the idea of a culture-free IQ test implausible, but so too is the idea of culture-free IQ (for discussion, see Muthukrishna & Henrich, 2016a). Indeed, the largest Flynn effect can be seen on the supposedly culture-free Raven's matrices (Nisbett et al. 2012; Flynn 2007), and on tests for fluid IQ rather than crystallized IQ (Pietschnig & Voracek, 2015). When it comes to heritability, subtests of IQ that are more culturally influenced are more heritable (Kan et al., 2013).

Beyond the diffusion of specific traits and abilities, a cultural evolutionary explanation also highlights how the Flynn effect is driven by the reorganization of cultural transmission pathways themselves. The introduction and improvement of formal schooling is one major instance of reorganization in cultural transmission that is also known to positively impact IQ (Ceci 1991; Brinch and Galloway 2012; Davis 2014; Ritchie and Tucker-Drob 2018). Greenfield (1998) describes how IQ scores in some rural US towns in the early 20th century increased rapidly at the same time as a number of coordinated changes in infrastructure, including better access to urban areas and new, high-quality road systems. Such enhancements in social connectivity directly translate into cultural connectivity, allowing for the influx and diffusion of psychological and behavioral traits that are considered valuable within the broader society. In much of the modern world, the kind of abstract information-processing ability measured by IQ tests is considered valuable, as it is useful in various white-collar professions that are typical of WEIRD societies. The Flynn effect therefore captures the progressive enhancements in cultural connectivity that have been occurring around the world due to improvements in various domains of infrastructure and technology including transportation, urbanization, education, and media. Global IQ rises in response to both the invention of relevant cultural traits and the enrichment of cultural transmission networks that carry those traits.

One clear test of this cumulative culture explanation for the Flynn effect would be to randomly assign children to attend or avoid formal schooling. Such a test would be highly unethical and differences in school attendance and quality are typically associated with various kinds of deprivation. Where policy changes have changed years of schooling in ways that lend themselves to causal identification through a natural experiment, an increase in formal education has been shown to cause an increase in IQ (Brinch & Galloway, 2012; Ritchie & Tucker-Drob, 2018). A recent test by Davis et al. (2020) offers even clearer data. Children, but not adult IQ performance is compared within age groups, because we assume children perform better as they get older. Exploiting a natural experiment where access to education was uncorrelated with SES, nutritional status and acculturation, Davis and colleagues show that without access to education, there is no correlation between age and IQ test performance. With moderate access, we see a moderate slope and with more access, a slope similar to the West.

Cultural Evolutionary Behavioral Genetics

Behavioral genetics offers a powerful empirical approach to understanding human behavior, but since the advent of whole-genome methods, its strategy appears to lean toward the notion that with enough data, ground truths about human nature and nurture, if only for some traits, will be revealed. Data alone is not enough (Muthukrishna & Henrich, 2019b); the thrust of our theoretical case is that human psychology and behavior have a large cultural component that has been changing over history (Boyd, 2018; Boyd & Richerson, 1985; Chudek et al., 2015; Henrich, 2016, 2020; Laland, 2018; Muthukrishna et al., 2021; Nunn, 2020; Wilson, 2019). Most recently our psychology has been shaped by the advent of writing, numeracy, different types of agriculture, the Industrial Revolution, the Internet, and smart phones (Domahs et al., 2010; Firth et al., 2019; Ong, 1982; Talhelm et al., 2014; Uskul et al., 2008; Wilmer et al., 2017). As new adaptive traits emerge (Muthukrishna & Henrich, 2016a), initially those who possess these traits will have an advantage, as in the case of access to new food sources, better healthcare, more efficient technologies, or easier methods of learning. But eventually the traits will reach fixation in the population through the processes of cultural diffusion (Henrich & Broesch, 2011; Muthukrishna et al., 2016b), at least until they are unseated by subsequent innovations (Kolodny et al., 2015; Muthukrishna & Henrich, 2016a). We predict that these cultural dynamics are reflected in heritability estimates.

As any geneticist knows, genetic heritability is a function of the variability in the environment, variability in genes, and variability in the phenotype. There is little to predict if the phenotype is homogenous, as in the number of fingers or kidneys. There is little to predict *with* if the environment or genes are homogenous. But what is factored into the environment includes not only the physical ecology, but also the cultural environment. While variance in genes and ecology may be relatively stable, the variance in the cultural environment is continually changing through the processes of cultural evolution. Genetic heritability estimates are highly affected by not only cultural diversity and cultural clustering, but also by factors that affect cultural transmission such as sociality (Muthukrishna et al., 2014), transmission fidelity (Morgan et al. 2015), tolerance for variation (Muthukrishna & Henrich, 2016a), population structure (Henrich, 2004a), and social network topology (Derex & Mesoudi, 2020; Muthukrishna & Schaller, 2020). Under most empirical conditions, behavioral genetics underestimates the contribution of culture, including in estimates of heritability. We don't disagree with the findings in these fields or the data used, but instead argue that more nuance is required in how they are interpreted. Our dual inheritance demands that a genetic account of human psychology and behavior must also account for culture and cultural evolution.

Toward a dynamic model of environment

We are surrounded by the products of culture yet are generally unaware of the generative processes that bring such complex objects and conditions into existence. Cultural transmission spans broad networks of interconnected individuals, as well as deep time scales of inheritance. Each individual experiences just a snapshot, leaving the global mechanics opaque. Thus, each of us is left with an intuition that *our* world is largely *the* world, which perhaps explains why the extent of the WEIRD people problem went unappreciated for so long, even a decade after publication of Henrich et al. (2010) (Apicella et al., 2020; Barrett, 2020; Nielsen et al., 2017; Pollet & Saxton, 2019; Tiokhin et al., 2019). From this limited vantage point, we evaluate questions such as the relative contributions of nature versus nurture. But our understanding of 'nurture' remains fundamentally anchored in our restricted experience of being enculturated into a particular environment, which leads us to implicitly see environmental features shared by members of our community as factors to be held constant, while our variables of interest—be they the absence of a parent, a childhood illness, birth into nobility, or a polygenic score—become matched to outcomes in our predictive models. Such models may be informal or formal, either encountered in community gossip ("children raised by single parents usually become…") or in scientific journals ("growth mindset interventions predict…"; Sisk et al. 2018[18]). Our need for causal explanations (Gopnik et al., 2004; Penn & Povinelli, 2007) meets our tendency to essentialize people and groups, where genes offer a better essentialist vehicle than the environment (Dar-Nimrod & Heine, 2011; Heine, 2017).

The importance of limiting behavioral genetic findings to the reference population was famously argued for by Lewontin (1970), and remains a caveat for the analysis of genetic effects.

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[18] As an aside, that growth mindset might only replicate among low-SES or at-risk students (if it replicates at all) fits with the general point that prediction is a function of variability. In this case, where there is a deficit, interventions may work, but where there is not, the potential gains are marginal or non-existent.

But it is far less appreciated that the reason why a multitude of phenotypic factors can be successfully held constant (or controlled for) in the first place is, in large part, due to the convergent force of cultural learning. Lewontin (1970), in his counterargument to Jensen's (1969) controversial article that argued for the innateness of IQ, used inbred corn and a uniformly acting nutrient solution as his rhetorical props for explaining the environmental sensitivity of genetic effects. Domesticated crops experience a more homogenous environment not by accident, but as a product of human cumulative culture. Lewontin's famous example is thus an unintentional illustration of how culture can generate at times extreme phenotypic convergence in significant features of the environment—either our own or of our domesticated flora and fauna.

We are all aware of gene–environment interactions (Hunter, 2005; Lewontin, 1970b; Moffitt et al., 2005), but we still tend to focus on what is predictive in our statistical models, which are constructed in a particular population, environment, and period of time but whose apparent lessons are commonly generalized beyond these contexts (e.g., the effects of an educational intervention). These models typically do not capture how the relevant environments are distributed within and between populations or how (or why) one type of environment transitions into another—'environment' is simply given as an exogenous variable. The cultural evolutionary approach forces us to explicitly recognize that human environments do not just happen to fall into place; they are rather the outcome of a dynamic, adaptive process that responds to both environmental and genetic factors. The literature on gene-environment interaction already recognizes genes and environments as non-orthogonal, but dependencies between the two are likely to be tighter and more prevalent than would be expected in a culture-free framework. This dynamic view of the environment also suggests that the problem of limited portability of polygenic scores across populations (Kim et al., 2018; Martin et al., 2017, 2019) is also likely to be a problem across historical time in a single population, as the issue is not just about differences in nucleotides across groups but also about the build-up of the cultural environment.

If we are to accommodate culture, the environment can no longer be treated as a static projection plane over which active elements (i.e., genes and G×E interactions) drop their shadows. Instead, both genes and environment—the latter animated by cultural dynamics—

are in motion with respect to each other (as an example, see language-brain coevolution; Christiansen 1994; Christiansen and Chater 2008; Deacon 1997; and cultural niche construction; Laland, Odling-Smee, and Feldman 2001; Laland and O'Brien 2011). An environment can be used as a reference frame against which to judge the effect of genes, but this is done for pragmatic purposes and not because environments are intrinsically fixed (Haworth and Davis 2014). We might take our cue from James Gibson's contribution to the study of vision, which he summarizes in the following manner:

> The standard approach to vision begins with the eye fixed and exposed to a momentary pattern of stimuli… The ecological approach to visual perception works from the opposite end. It begins with the flowing array of the observer who walks from one vista to another, moves around an object of interest, and can approach it for scrutiny, thus extracting the invariants that underlie the changing perspective structure (Gibson 1979, p.303).

Gibson recognized that environmental change is not noise, but rather the very medium through which the scientist obtains knowledge about visual function. Our argument presents an analogous approach to the study of genes.

Toward a culturally situated understanding of intelligence

The genetic underpinnings of intelligence have roots going back to the beginning of behavioral genetics (Galton, 1869, 1874) and have been fiercely debated since at least Jensen (1969) and Lewontin (1970). The topic remains contentious, but a dual inheritance perspective cuts through some of this debate. Here we summarize some key points.

IQ appears heritable—often measured at around 0.4 in toddlers and increasing up to 0.7 or 0.8 in adults (Bergen et al., 2007; Bouchard, 2009). But as we and others have discussed, a high heritability score does not necessarily tell us whether a trait is primarily genetic; high heritability can also be an indicator of environmental homogeneity. Intelligence is a function of both our hardware (brain) and our software (culture) (Heyes 2018; Hutchins 1995; Vygotsky 1980), and the software has been changing far more and far more rapidly than has the hardware

(Uchiyama & Muthukrishna, in pressb). Genes certainly contribute to the size and organization of our brains—indeed, the Cultural Brain Hypothesis predicts a strong selection pressure for larger brains (Muthukrishna, Doebeli, et al., 2018a), still evident in the rapid increase in emergency birth interventions as a function of head size (Lipschuetz et al., 2015a). But those genes are explaining residual phenotypic variation only after accounting for environmental factors that also affect the quality of neural hardware, such as nutrition (Lynn, 1990; Stoch et al., 1982), parasites (Jardim-Botelho et al., 2008), air pollution (X. Zhang et al., 2018), and lead exposure (Needleman & Gatsonis, 1990; Wasserman et al., 1997). All are known to influence intelligence, but in societies that have been able to minimize variation on such factors through cultural diffusion, the environmental effect is also minimized. And it is not only such physical and physiological variables: changes in and diffusion of the cultural package delivered by schooling (Ceci 1991; Davis 2014; Ritchie and Tucker-Drob 2018; Davis et al. 2020) and our ever more complex entertainment media (Johnson 2006; Greenfield 2009) also reduce the variation to be explained. All these processes unfold outside of any genetic changes to our neural hardware.

Recent, high-powered GWAS have found that genes associated with intelligence are expressed predominantly in the central nervous system (Sniekers et al. 2017; Savage et al. 2018; Davies et al. 2018), but these findings too only explain the residual variation that remains after cumulative culture has reduced variation across many other variables—such as pathogens, parasites, and nutrition—that would otherwise account for huge portions of variation on IQ test performance. The expression of "intelligence genes" may cluster inside the head (Savage et al. 2018; Davies et al. 2018; Sniekers et al. 2017), but this expression profile cannot be meaningfully evaluated without first considering the prior contributions of cumulative culture, which are invisible to standard methods in behavioral genetics. We predict that in general, the set of identified genes that explain human traits such as intelligence is liable to change as a result of cumulative cultural evolution, both across cultures and across time within a single culture. Gene–phenotype mappings for culturally modifiable traits in humans are typically more transient than they are in other species, whose gene–phenotype mappings will typically (but not exclusively; see niche construction Laland, Matthews, and Feldman 2016) only change at the slower timescales of genetic evolution or of passive ecological change. Just as limited sampling across historical time has obscured this difference in the temporal horizon of genetic effects across humans and nonhuman animals, the WEIRD sampling problem has obscured differences between humans and nonhumans with respect to within-species generalizability as well.

Even if intelligence is highly heritable in humans, this does not indicate that its genomic substrate works independently of the environment. The cultural environment can amplify heritability, and the degree of this amplification covaries with the extent to which a society has been able to reduce variation in physical, physiological, and informational factors that impact the phenotype. Developed countries, almost by definition, have been most successful in reducing this variation. This flattening of variation is an outcome brought about by expanded networks of cultural influence and greater cultural connectivity, both due in part to technological innovation and in part to culturally evolving social norms and institutions. High heritability of intelligence is therefore most likely to reflect the effect of the cultural environment in these societies. As we argue in our discussion of the Flynn Effect, cultural traits associated with high IQ are themselves transmitted through these cultural networks.

If a society demonstrates high heritability of some trait together with a high relative level of the trait, this combination may give the strong impression of genetic advantage, but the argument that we have developed in this target article points to a different kind of explanation. Comparisons of mean IQ across countries, or 'National IQ' (Lynn & Vanhanen, 2012), have been under scrutiny recently, but apart from the various methodological flaws that have been pointed out (e.g., Ebbesen 2020), the non-obvious role of the cultural environment in shaping both the trait and its measurement should be seriously considered in this discussion as well. Epistemic issues like the cultural Simpson's paradox should also be considered in cross-national analysis, as it can create associations between groups and traits that are a product of the cultural environment even when it appears otherwise. The examples that we use to illustrate the paradox— vitamin D deficiency and excess winter mortality (Section 3.4)—are easy to grasp, but actual instantiations of the cultural Simpson's paradox are likely to be less straightforward.

The cultural evolutionary framework possesses unique strength in providing these kinds of explanatory strategies, as well as a general theoretical basis for understanding the formation and distribution of psychological traits such as intelligence. The approach that we develop here builds upon earlier, culturally situated approaches to intelligence (Berry 1972; Greenfield 1998; Cole 1998; Vygotsky 1980; Nisbett 2009), but goes further in incorporating the population dynamics of cumulative culture, which offers greater clarity in how traits like IQ are shaped by non-genetic processes that span generational time.

Conclusion

> *Genetics is indeed in a peculiarly favoured condition in that Providence has shielded the geneticist from many of the difficulties of a reliably controlled comparison. The different genotypes possible from the same mating have been beautifully randomised by the meiotic process. A more perfect control of conditions is scarcely possible, than that of different genotypes appearing in the same litter.* (Fisher, 1952)

Above, Sir Ronald Fisher exalts the inferential purity that is afforded by the powerful pairing of sexual recombination with simultaneous multiple birth, which conveniently flattens environmental variation. But of course, this purity becomes progressively degraded with age, as environmental effects channel offspring through different developmental trajectories. Even among inbred, genetically identical mice who cohabit an experimentally controlled space, self-organizing trajectories of environmental experience result in clear differentiation in phenotypes like exploration, sociality, play behavior, and postnatal neurogenesis (Freund et al., 2013, 2015; Shemesh et al., 2013).

Humans trajectories differentiate so much more. We inhabit almost every ecosystem on Earth, not by speciating as many animals do, but through cultural adaptation, opening different developmental pathways in different societies. But even within a single society, our massive specialization leads to high levels of differentiation. Our genetic variation explains some of this, but we are the least genetically diverse great ape—two groups of chimpanzees in the Congo are more genetically different from each other than two groups of humans plucked from Berlin and Beijing (Prado-Martinez et al., 2013). Most of our diversity is cultural rather than genetic (Bell et al., 2009; Muthukrishna et al., 2020a); culture drives much of our within-species phenotypic variation. At best, genetic effects can only be specified within the ambit of a specific cultural context, but even the boundaries of that context cannot be specified without cultural evolutionary tools. And because culture is also evolving over time, these cultural contexts also require a timestamp. Heritability is not a property of a trait in itself, because in the absence of a reference culture it is necessarily unstable.

Cultural evolution yields cultural clusters. Within each society, environments are relatively homogenous, and the homogeneity that we find within societies is coupled with pronounced heterogeneity between societies (Bell, Richerson, and McElreath 2009; Richerson et al. 2016). Extrapolating genetic effects beyond a species is obviously mistaken, but so too is extrapolating a genetic effect beyond a culture. But this is what researchers have been doing since Galton, and it is ingrained in both our methodology and our thinking, culminating in the recent triumphalist discourse surrounding behavioral genetics and GWAS[19]. The movement toward more diverse genomic data ought to make some of these problems more obvious, just as more diverse psychological data made the problems of WEIRD psychology more obvious. But here too, data alone will not solve the problem (Muthukrishna et al., 2020a; Muthukrishna & Henrich, 2019b). The question is not whether genes or culture contribute more to a behavioral trait, as behavioral traits can only be understood as emergent products of our dual inheritance, genetic and cultural. Nothing in behavioral genetics makes sense except in the light of cultural evolution.

Appendix: Modeling the Effect of cultural evolution on heritability

Variance partitioning model

Here we describe a simple mathematical model that captures the relationship between cultural evolution and heritability. Cultural evolution is a process in which some cultural variants spread through a population more prolifically than others. This spread can be partly

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[19] Some recent prominent examples that have entered the public discourse include Plomin (2019) and Murray (2020). Plomin states, “Polygenic scores are the ultimate psychological test because, for the first time, they can tell our genetic fortunes.” Similarly, Murray declares: “By the end of the 2020s, it will be widely accepted that quantitative studies of social behavior that don’t use polygenic scores usually aren’t worth reading. More formally, it will be widely accepted that the predictive validity of polygenic scores gives us useful information about causes even though we still don’t understand the causal pathways.”

due to intrinsic differences in the trait (e.g., steel axes are better than stone axes) and partly due to social learning strategies like the conformist bias, success bias, and prestige bias (for summary, see Kendal et al. 2018; Chudek, Muthukrishna, and Henrich 2015). Such strategies vary in their rules for selecting what to learn or whom to learn from, but they all lead to the disproportionate adoption of particular cultural variants over others, and thus to a reduction in the population-level variability of behaviors. Individual incremental improvement, individual learning (Rogers 1988; Legare and Nielsen 2015), cultural transmission error, recombination of cultural traits, and other sources of innovation (Muthukrishna & Henrich, 2016a) will continue to inject novel variants into the population, but the fact that a nearly unrestricted number of learners can inherit the behaviors and ideas of a few influential individuals makes it easy for cultural transmission to induce homogeneity. It is not only behavioral traits that become similar within a population through cultural transmission, but also environmental factors that shape behavioral traits, such as nutrition, sanitation, education, and media.

Heritability is defined as the proportion of phenotypic variance for some trait that is explained by genes. For broad-sense heritability, $H^2 = V_G/V_P$, where H^2 is heritability, V_P is the variance in phenotype, and V_G is the phenotypic variance explained by all genetic factors including additive genetic variance, dominance interactions, and epistatic interactions. Because total phenotypic variance is made up of contributions from both genes and environment ($V_P = V_G + V_E$), a reduction in the environmental contribution necessarily increases heritability; cultural evolution has been a powerful force for behavioral homogenization and hence reduction in environmental variance over human history. Behavioral geneticists partition phenotypic variance into genetic and environmental components, but here we further partition the environmental component into environmental variation unaffected by cultural evolution (e.g., UV exposure due to geographic location) and environmental variation affected by cultural evolution (e.g., UV exposure due to sunscreen use). For convenience, we refer to the former as the ecological environmental variance component and the latter as the cultural environmental variance component, and represent this partition using the following notation:

$$(1)\quad V_E = V_e + V_c$$

where V_e and V_c denote the phenotypic variance explained by ecology and culture, respectively.

In reality, the cultural environment and even individual cultural traits will typically have a high-dimensional variance structure, such as with the various components of a tool or a ritual that can be independently modified, but here we employ a unidimensional space of cultural variation. For simplicity, we model cultural environmental variation as a uniform continuous distribution that is bound by k_{min}, the most unfavorable environmental state (for some given phenotype) within the experienced range of environments, and k_{max}, the most favorable. We can use the theoretically expected variance of the continuous uniform distribution ($\frac{1}{12}(b-a)^2$, where *a* and *b* are the minimum and maximum values) to rewrite (1):

$$(2)\quad V_E = V_e + \tfrac{1}{12}(k_{max} - k_{min})^2$$

We can then substitute (2) into the standard formula for broad-sense heritability:

$$(3)\quad H^2 = \frac{V_G}{V_G + V_e + \frac{1}{12}(k_{max} - k_{min})^2}$$

Heritability thus decreases when $(k_{max} - k_{min})$ is large and increases when it is small. The smaller the experienced range of aspects of the cultural environment that contribute to phenotypic variation, the more phenotypic variation there is left to be explained by genes and by consequence, the higher the heritability. The magnitude of this cultural effect depends upon (i) the ratio of V_c to V_e, which is the extent of cultural influence upon the environmental variance component as a whole, as well as (ii) the ratio of genetic influence to total environmental influence (V_G to V_E). We illustrate the effect of each of these variance components on heritability in Figure 3.4. To keep the model simple, we omit the gene–environment interaction and gene–environment correlation terms.

This model shows how heritability can be shaped by a shifting cultural environment. Once again, this insight is in itself neither new nor surprising. But the model we describe here allows us to go further and consider the particular, systematic ways in which the cultural environment is expected to change. Although this model does not incorporate cultural dynamics as such, we can nonetheless map two broad cultural dynamics onto its framework: (1) new innovations elevating the upper bound of cultural complexity (Henrich, 2004a; Muthukrishna & Henrich, 2016a) and (2) diffusion of these innovations (Rogers 2003;

Henrich 2001; Comin and Hobijn 2010)—new traits emerge and then spread to fixation in the population. Within this framework, we can think of increases in cultural complexity as pushing up k_{max}, the most favorable cultural conditions in a society. In turn, we can think of diffusion as pushing up k_{min}, the most unfavorable cultural conditions in a society. As an example, imagine k_{max} is the educational contribution of the best school in a society and k_{min} is the educational contribution of the worst school in a society. In some societies, educational innovations diffuse quickly, whereas in others, there is more lag between the discovery of a new technology or pedagogical technique and its widespread adoption. Some societies are highly equal ($k_{max} - k_{min}$ is small) and others are more unequal ($k_{max} - k_{min}$ is large). The magnitude of the lag between increasing k_{max} and k_{min}—for example, how quickly educational innovations in the best schools diffuse to other schools—impacts environmental heterogeneity and thus heritability: we illustrate this effect as different trajectories of cultural change in Figure 3.4c. Moreover, by further decomposing k_{max} and k_{min}into their governing cultural dynamics, we can predict the trajectories of heritability over time.

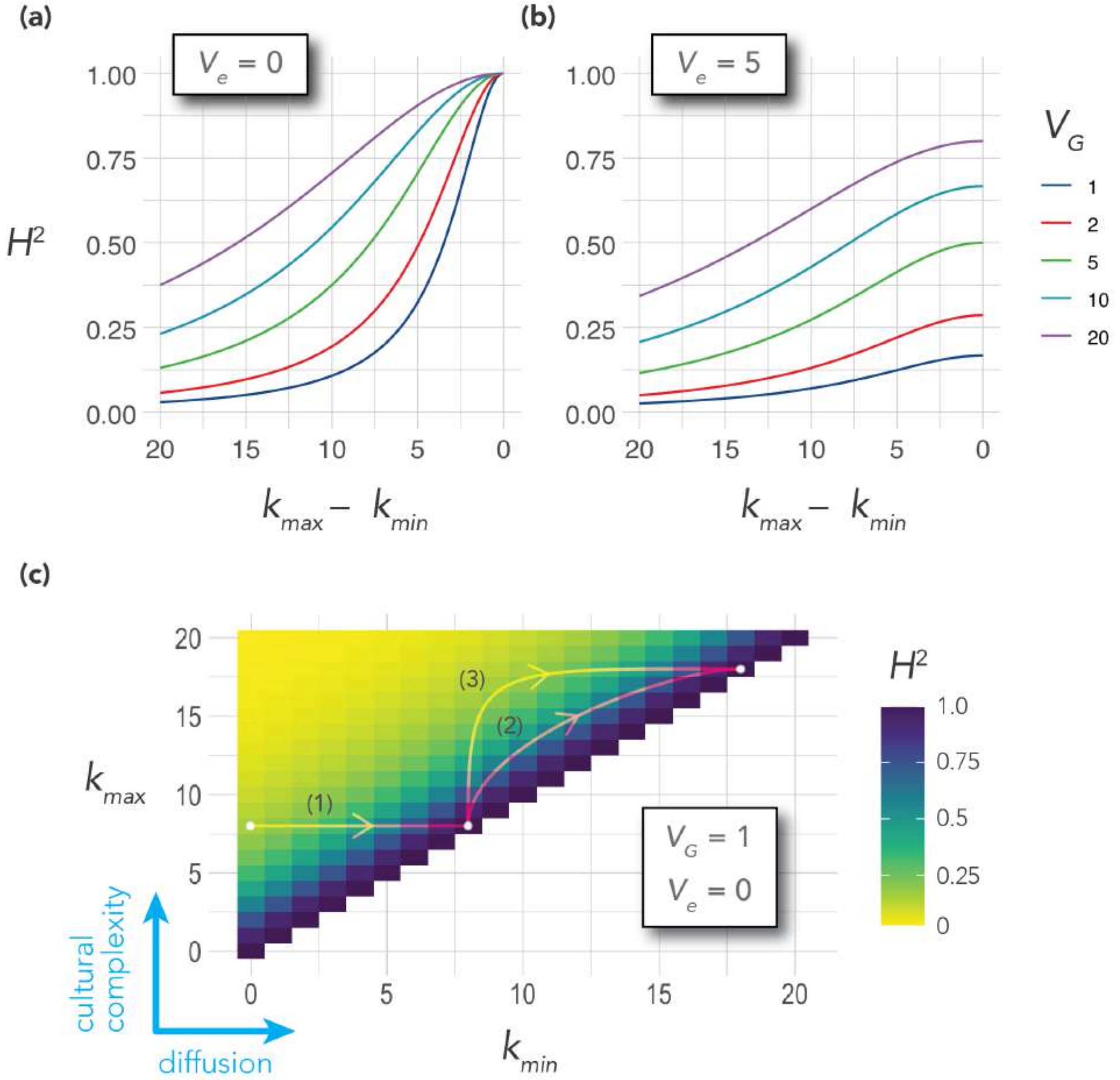

Figure 3.4: Visualizations of Equation 3. Heritability curves as a function of cultural range ($k_{max} - k_{min}$) and of the amount of genetic variance (V_G). (a) Values are computed for $V_e = 0$ (the environment is entirely explained by cultural factors) and (b) for $V_e = 5$ (some of the environment is explained by non-cultural factors, such as climate). (c) An alternative visualization in which we look at the absolute values of k_{max} and k_{min} rather than just their difference, plotted for $V_e = 0$ and $V_G = 1$. An increase in k_{max} expands environmental variation and implies increasing maximum cultural complexity, whereas an increase in k_{min} reduces environmental variation and implies diffusion. Trajectory 1 represents a society's transition from a more unequal cultural environment to a more equal cultural environment, but with no increase in cultural complexity. Trajectories 2 and 3 represent a simultaneous increase in cultural complexity and diffusion of the newly established complex traits, where a rising k_{max} pulls k_{min} upward but with varying lags: for trajectory 2 there is little lag between increase in the complexity of the culture and its spread, whereas for trajectory 3 there is considerable lag, with a longer period of relative cultural inequality. Genetic heritability decreases with rising cultural complexity and increases with cultural equality (diffusion). For example, continued innovation will reduce heritability up to the point at which the society is maximally unequal, and then increase heritability once more as the cultural innovations spread to the entire population—i.e., curves 2 and 3 are non-monotonic.

Cultural dynamics model

To capture the effect of a changing cultural environment on heritability estimates over time, we construct a simple model that incorporates a time axis and whose parameters can be adjusted to compare different cultural trajectories. This dynamic model builds upon the previous variance partitioning model, but extends it by representing k_{min} and k_{max}—the upper and lower bounds of the acquired range of cultural complexity—as sigmoidal trajectories (s-shaped curves), which are commonly used to model cultural diffusion (Rogers 2003; Henrich 2001). Here we use the Gompertz function, which is a special case of the generalized logistic function that is commonly used in biology to model growth. In particular, we employ the following re-parameterization of the Gompertz that is given by Tjørve and Tjørve (2017):

$$\text{(4)} \qquad k_{min} = k_0 \left(\frac{k_0}{A}\right)^{\exp\left(-e\beta_{k_{min}} t/A\right)-1}$$

$$\text{(5)} \qquad k_{max} = k_0 \left(\frac{k_0}{A}\right)^{\exp\left(-e\beta_{k_{max}} t/A\right)-1}$$

where t is time; A is the upper asymptote of both k_{min} and k_{max}; k_0 is a parameter that fixes both k_{min} and k_{max} to a particular value at $t = 0$; and $\beta_{k_{min}}$ and $\beta_{k_{max}}$ are the maximum growth rates of k_{min} and k_{max} respectively. At any given time point, $k_{min} \leq k_{max}$ by definition: this condition is satisfied for all $t \geq 0$ (but not for $t < 0$) when we set $\beta_{k_{max}}$ to be larger than $\beta_{k_{min}}$, due to both curves being fixed to the same value k_0 at $t = 0$. This model therefore requires that k_{min} and k_{max} only be evaluated over non-negative time points.

The parameters $\beta_{k_{min}}$ and $\beta_{k_{max}}$ determine the shapes of the diffusion and innovation curves respectively. They indicate maximum (absolute) growth rates, which occur at the inflection points of k_{min} and k_{max}. In a Gompertz function, inflection occurs at $\frac{1}{e} = 36.79\%$ of the upper asymptote value A, regardless of parameter values. Therefore, curves with a larger maximum growth rate are steeper and approach the asymptote more rapidly. By adjusting $\beta_{k_{min}}$ and $\beta_{k_{max}}$, we can model the variation in relative rates of cultural innovation and diffusion across different types of society, as well as the impact of these different cultural trajectories on heritability. Many factors can affect these rates of innovation and diffusion (De et al., 2017; Gelfand, 2018; Kolodny et al., 2015; Muthukrishna & Henrich, 2016a; Muthukrishna & Schaller, 2020; E. M. Rogers, 2003; Schaller & Muthukrishna, in press). For example, a "tight" society may have low rates of radical innovation, high rates of incremental innovation, and high rates of diffusion of these innovations, whereas a "loose" society may have high rates of radical innovation but lower rates of diffusion (Gelfand, 2018). Other societies may be high or low in both. In Figure 3.5 we illustrate a 2×2 of societies that vary in their innovation and diffusion rates.

Heritability is computed using the same procedure as the variance partitioning model, but dynamically. Following equation (2), we compute the cultural variance component V_c at time t by taking the variance of the uniform distribution over the interval $[k_{max}, k_{max}]$ at time t. Phenotypic variance explained by the environment (i.e., ecology and culture) at time t therefore takes the following form:

$$(6) \qquad V_{E(t)} = V_e + \tfrac{1}{12}(k_{max(t)} - k_{min(t)})^2$$

where V_e is again the ecological variance component, which we treat as static compared to the rapidly changing cultural environment. By selecting values for both V_e and V_G (the genetic variance component), we can thus compute broad-sense heritability at time t in the same manner as (3):

$$(7) \qquad H^2_{(t)} = \frac{V_G}{V_G+V_e+\frac{1}{12}(k_{max(t)}-k_{min(t)})^2}$$

These dynamics of changing environmental variance and heritability were only implicitly included in the variance partitioning model above (see Figure 3.4c) but are represented here explicitly. The effect of innovation and diffusion on cultural variance and heritability are illustrated in the lower panels of each society in Figure 3.5. These results show, for example, that societies with both rapid innovation and rapid diffusion of these innovations should experience large transient changes in heritability (Figure 3.5a), while a combination of slow innovation and rapid diffusion has little impact on heritability (Figure 3.5c). Societies with rapid innovation but long lags in diffusion will experience large changes in heritability over longer time scales (Figure 3.5b), as will societies with slow innovation and slow diffusion

(Figure 3.5d). In reality, there may be multiple relevant cultural innovations for some given phenotypic trait at any given point in time—under such a scenario, heritability would tend to fluctuate around some intermediate value rather than traverse the full range depicted in the lower panels of Figure 3.5. The output of this model predicts that on average, heritability of culturally transmissible traits should be higher in more homogenous (tight or less clustered) societies than in less homogeneous (loose or more clustered) societies, as discussed in Section 2.2.3.

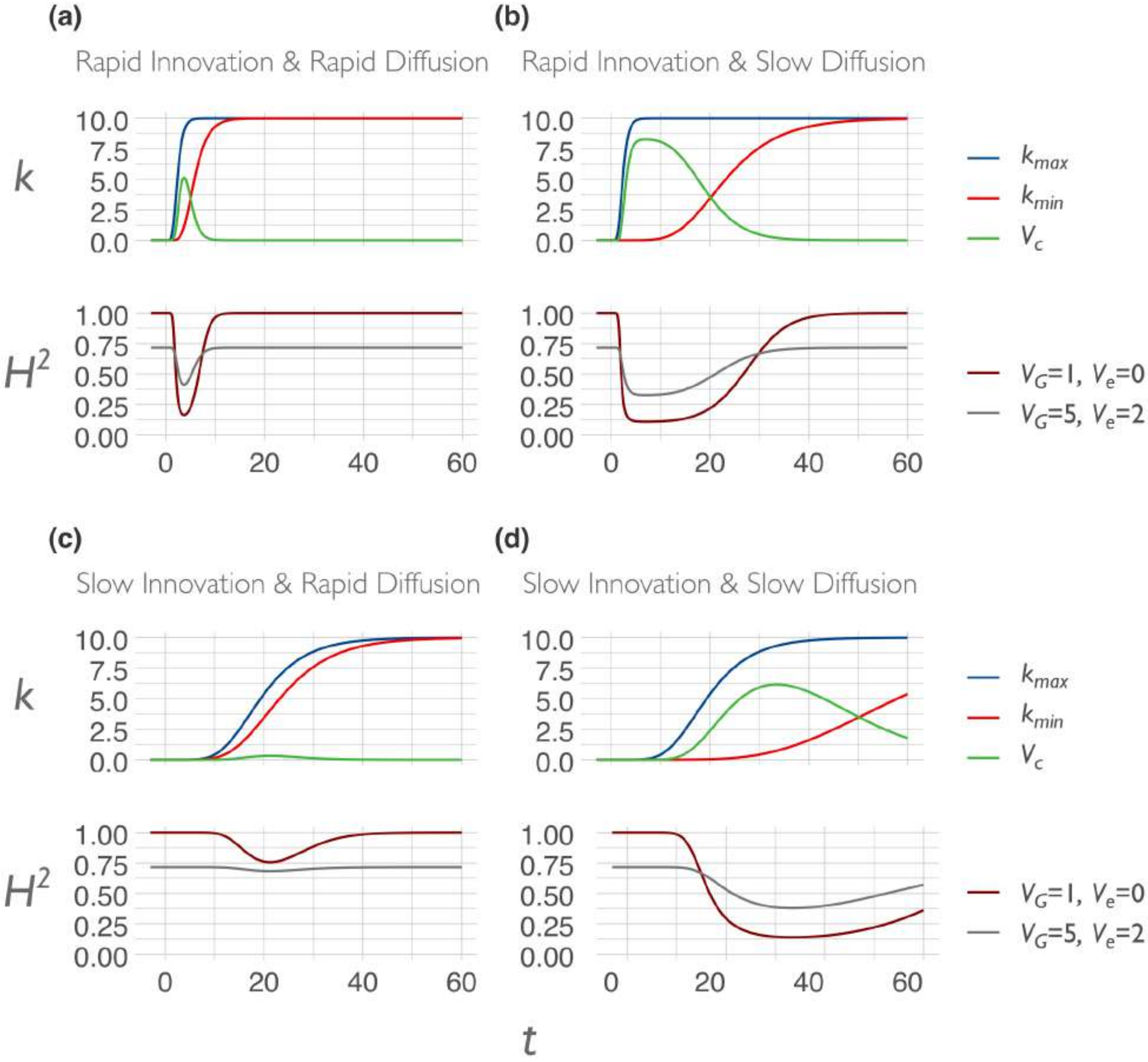

Figure 3.5: Output examples of the cultural dynamics model, for 4 prototypical societies. For each society, the upper panel displays the change over time in the lower (k_{min}) and upper bounds (k_{max}) of the society's cultural complexity as it pertains to some given phenotypic trait, together with the variance explained by the cultural

environment V_c, which is the theoretically expected variance of the uniform distribution over the interval $[k_{min}, k_{max}]$. The lower panel displays the change in heritability over time under two different settings for genetic and ecological variance components. Global model parameters are set to $A = 10$ and $W_0 = 10^{-6}$. (a) A society that innovates rapidly while also diffusing these innovations across the population rapidly; maximum growth rates of k_{min} and k_{max} are $\beta_{k_{min}} = 2$ and $\beta_{k_{max}} = 5$, respectively. (b) A society that innovates rapidly but whose innovations are slow to diffuse; $\beta_{k_{min}} = 0.5$ and $\beta_{k_{max}} = 5$. (c) A society that innovates only gradually but whose innovations diffuse quickly; $\beta_{k_{min}} = 0.5$ and $\beta_{k_{max}} = 0.6$. (d) A society that innovates only gradually and whose innovations take even longer to diffuse; $\beta_{k_{min}} = 0.2$ and $\beta_{k_{max}} = 0.6$.

Chapter 4: Cultural variance reduces the heritability of psychological, behavioral, and psychiatric traits

Introduction

Heritability, the proportion of phenotypic variance explained by genes, has long played an important role in debates about nature and nurture. By boiling down the statistical relationship between genetic relatedness and phenotypic similarity into a single standardized estimate, heritability offers an intuitive and easily communicable measure of genetic effect. Heritability has been a source of both insight and controversy. Many authors have written about the misunderstandings and simplifications that regularly occur when interpreting this statistic (Feldman & Ramachandran, 2018a; Haworth & Davis, 2014; Lewontin, 1974b; Visscher et al., 2008; Vitzthum, 2003). Such errors in interpretation commonly lead to the reification of heritability as an intrinsic index of innateness, where highly heritable traits are understood to be genetically "hardwired" and relatively impervious to input from experience.

Heritability depends upon the amount of variation in phenotype, genes, and environment, and on gene–environment interactions and correlations, and is sensitive to changes in any of these components. Due to this sensitivity, behavioral geneticists have been warning against the extrapolation of heritability from one population to another at least since the arguments of Lewontin and Feldman (M. Feldman & Lewontin, 1975; Lewontin, 1970b, 1974a). Their message was clear: due to gene–environment interactions, a genetic effect can only be understood within the environment in which the effect was originally observed. Environmental conditions vary across societies in both obvious and subtle ways. Due to a WEIRD (western, educated, industrialized, rich, democratic) sampling bias in behavioral genetic studies (Uchiyama et al., forthcoming), the true extent of this variation is unclear, but differences in environmental factors are likely to be part of the explanation for the limited portability of genetic effects across populations, most recently seen in polygenic scores (M. S. Kim et al., 2018; A. R. Martin et al., 2017, 2019). Much of the environmental variation across human societies can be attributed to cultural variation and the myriad differences in practices, norms, artifacts, and beliefs that come with it.

Cultural variation arises through the dynamics of cultural evolution. In contrast to genetic evolution, cultural evolution confers adaptive phenotypes through processes of social learning such as selective imitation and conformist learning (Boyd & Richerson, 1985; L. L. Cavalli-Sforza & Feldman, 1981a). Although other animals such as some birds, primates, and whales also exhibit impressive displays of cultural transmission (Aplin, 2019; Faust et al., 2020; Fox et al., 2017b; Whiten, 2019), the complexity of human culture far outstrips that of any other species, due to features like high transmission fidelity and an enhanced capacity for the accumulation of trait modifications over generations, known as cumulative culture (Dean et al., 2014a; Henrich, 2004a). Indeed, culture is a defining characteristic of our species, even feeding back onto our genetic make-up, as seen for example in how our jaws are too weak and our guts too short for a world without cultural learning of skills like the control of fire and cooking (Aiello & Wheeler, 1995a; Wrangham, 2017). These anatomical changes are inscribed in our genome, but the environmental niche that selects for the genetic profile is carved out by cultural dynamics, a process known as culture–gene coevolution . Therefore, whereas in most species digestive function is carried out entirely by the products of genetic evolution (including by the microbiome), for humans a substantial part of this functional pathway is taken outside of the organism and carried out by products of cultural evolution, including things like ovens, cutting techniques, and knowledge of fermentation. Cultural adaptations and genetic adaptations thus overlap within a common space of biological function, where cultural evolution proceeds at a considerably more rapid pace than genetic evolution. Due to this functional overlap, culture and genes can become easily confounded when using research methods that are sensitive to only one or the other.

For instance, the heritability of IQ is commonly reported to be around 0.4 in toddlers and increasing up to 0.7 or 0.8 in adults (Bergen et al., 2007; Bouchard, 2009), but note that these numbers capture only the residual phenotypic variance that remains to be explained by genes after cultural evolution has run its course. Cultural evolution has mitigated many environmental factors that are known to negatively impact IQ, such as malnutrition (Lynn, 1990; Stoch et al., 1982), parasite infection (Jardim-Botelho et al., 2008), and lead exposure (Needleman & Gatsonis, 1990; Wasserman et al., 1997). It also works in the opposite direction when cultural evolution builds up technologies and institutions that promote IQ, such as schooling (Ceci 1991; Davis 2014; Ritchie and Tucker-Drob 2018; Davis et al. 2020). Despite being substantial, such cultural effects do not appear in heritability estimates, being captured in neither the genetic nor environmental components. This is due to cultural transmission being a victim of its own success: when cultural traits are efficiently propagated, this flattens the population variation of the trait, leaving less phenotypic variance to be explained by environmental factors and proportionally more to be explained by genes. It thus appears as if the cultural environment has little role to play in comparison to genes, when in fact the opposite may be true. The heritability statistic veils cultural effects in this manner, making it difficult to assess the relative contributions of genes and culture (as well as the non-cultural environment) with respect to phenotypic formation (Uchiyama et al., forthcoming).

However, societies likely vary in the extent to which they flatten population variation of cultural traits. Some societies prefer uniformity in behaviors and strict adherence to norms, while others are more tolerant of deviation, even when most deviations end poorly (Gelfand et al., 2011a; Gelfand, 2018; Henrich, 2004a; Muthukrishna & Henrich, 2016a). We would expect greater cultural variance—i.e., variance in the population distribution of cultural traits—in the latter type of society than in the former. Therefore one strategy would be to leverage such cross-cultural differences in cultural variance to test for a relationship between cultural variance and observed heritability. Greater cultural variance should be linked to a larger role for the environmental component of phenotypic variance and thus lower heritability, but only for traits that are culturally transmissible. A culturally transmissible trait is one whose population distribution can be shaped by cultural dynamics, analogous to how the population distribution of genetic variants get shaped by selection, drift, mating structure, and mutation rate. Among the traits studied in the field of behavioral genetics, psychological and behavioral traits are much more likely to be culturally transmissible than anatomical and physiological traits. We thus predicted a negative relationship between the amount of cultural variance in a society and the observed heritability of psychological and behavioral traits. This is one prediction among several that we describe elsewhere in greater detail (Uchiyama et al., forthcoming).

In the present study, we test this prediction by conducting cross-national comparisons between indices of cultural variance derived from survey data and heritability estimates drawn from a comprehensive meta-analysis of twin studies. Because the twin study data set covers a period of 54 years, many dozens of phenotypes, varying methodologies, and 14 countries, but all of this over a relatively small sample size, we expected a large amount of noise in our data. We thus focused on evaluating the directionality and robustness of the effect, employing a specification curve analysis (Simonsohn et al., 2020) with preregistration of analytical procedures and hypotheses (available at https://osf.io/brdct).

Results

To gather data on heritability, we drew upon a meta-analysis that covers virtually all twin studies published between 1958 and 2012 (Polderman et al., 2015b) and separated the contained traits into three groups. The first group was the *inclusive* set of culturally transmissible traits, consisting of traits whose population distribution we judged could be shaped by cultural transmission. These traits consisted broadly of psychological, behavioral, and psychiatric traits. The second group was the *restricted* set of culturally transmissible traits, which was identical to the inclusive set except with psychiatric traits omitted—a decision based on our initial uncertainty about whether psychiatric traits would behave in the same manner as psychological and behavioral traits that were non-clinical. The remaining traits that were not included in either the inclusive or restricted sets were gathered into an *acultural* set of traits, which we judged likely to be less culturally transmissible. Included here were various anatomical and physiological (e.g., immunological, endocrine, neurological, circulatory) traits, many of which are clinical disorders, as well as a few traits whose labels at first appeared to be psychological in character (e.g., "experience of self and time") but upon closer inspection were judged not to be.

This pre-registered grouping yielded 362 observations in the inclusive set, 118 observations in the restricted set, and 301 observations in the acultural set, where each observation was a published twin heritability estimate. Not all of these heritability estimates could be used in the subsequent analyses, as some were from countries that were missing cultural variance scores for one or more of the cultural variance indices. We therefore conducted an additional analysis in which we imputed missing cultural variance scores, and employed this variation in method to test for robustness of the results (discussed in further detail below in this section and in **Methods**).

Figure 4.1 displays the distribution of heritability estimates for the restricted set and is organized by trait (i.e., ICF/ICD-10 subchapter). **Figure 4.2** displays heritability estimates in the same manner but only for psychiatric traits. The union of the restricted set and the psychiatric set constitutes the inclusive set of traits. The distribution of the country of observation for all samples in the inclusive set is displayed in **Figure 4.3**.

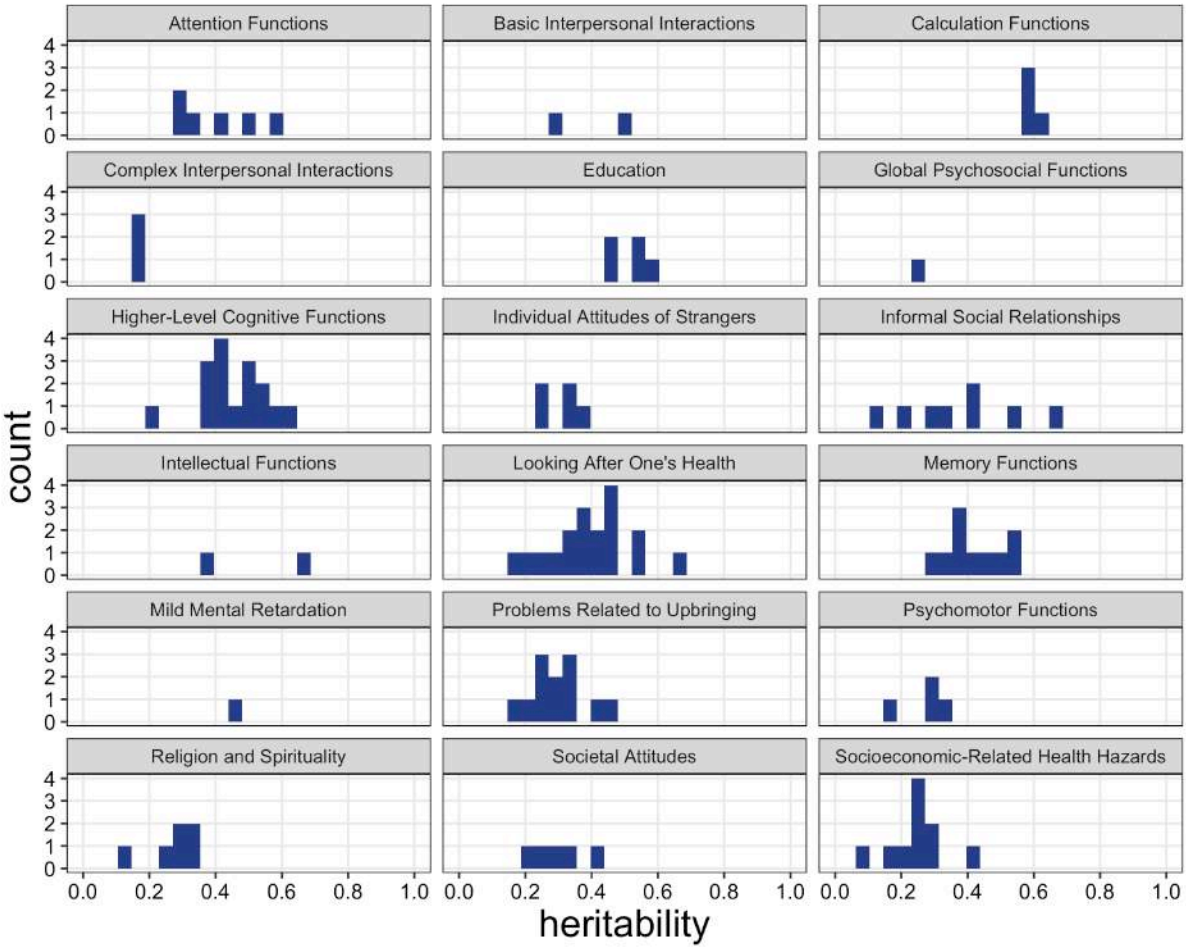

Figure 4.1: Histograms of all 118 observations that fall under the restricted set of culturally transmissible traits, across 18 traits labelled at subchapter granularity. Some trait names have been shortened to facilitate visual presentation.

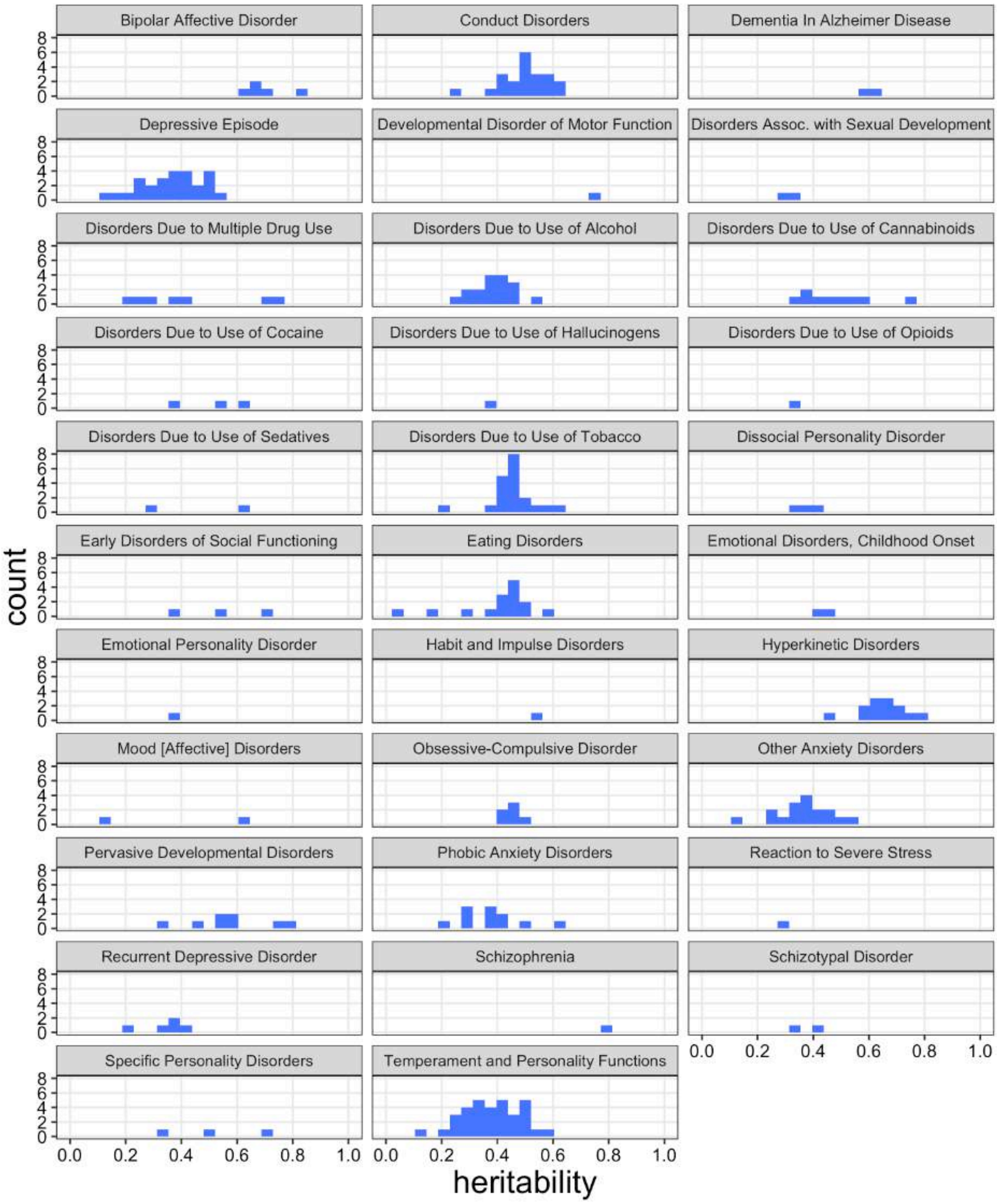

Figure 4.2: Histograms of all 244 observations that make up the psychiatric traits, across 32 traits labeled at Subchapter granularity. These traits combined with the traits of the restrictive set of traits (Figure 4.1) jointly constitute the inclusive set of traits. Some trait names have been shortened to facilitate visual presentation.

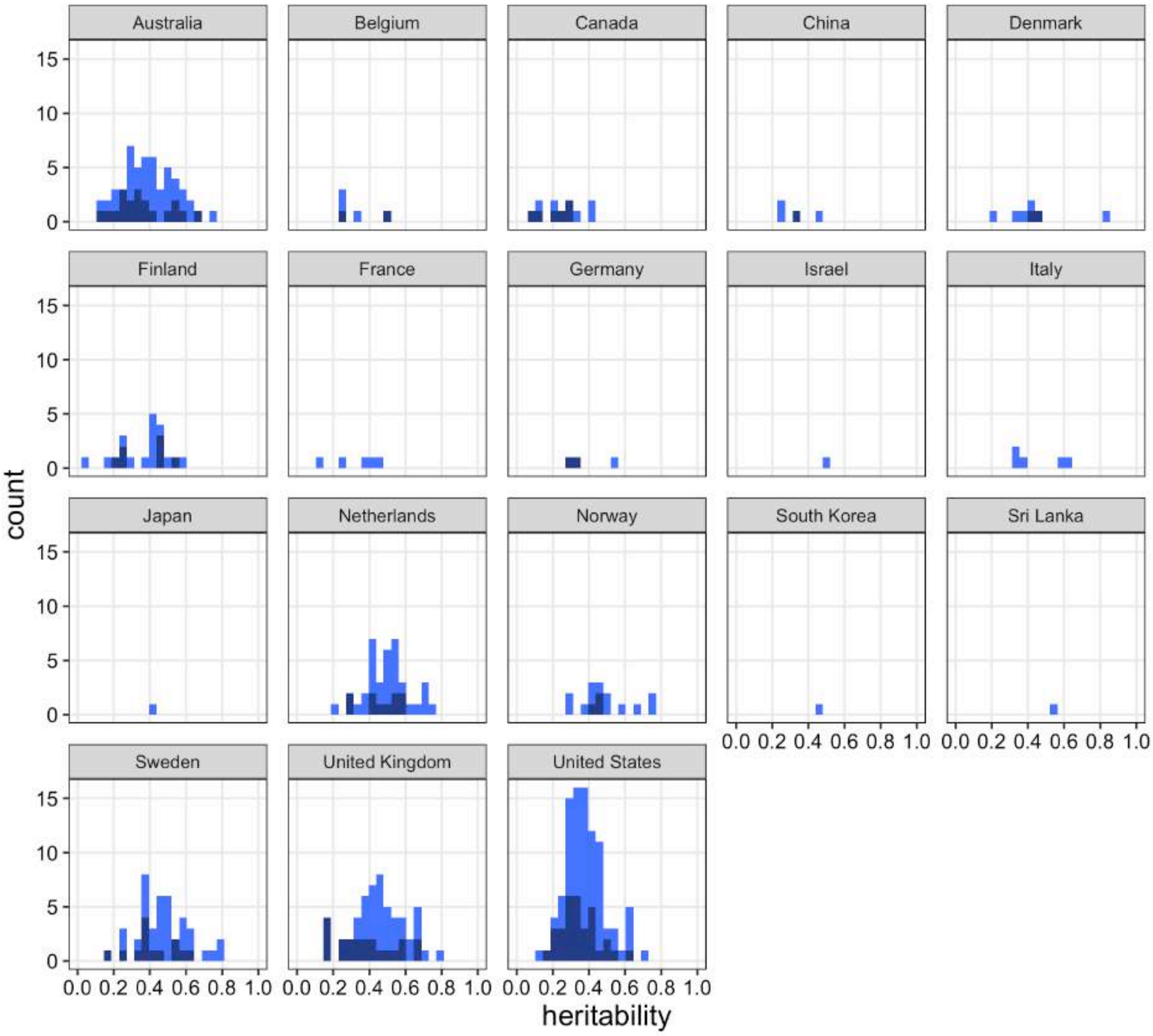

Figure 4.3: Histograms of the 362 observations that fall under the inclusive set of traits, across the 18 countries represented in this analysis. Following the color scheme of Figures 4.1 and 4.2, observations linked to the restricted set of traits is marked in a darker shade of blue and observations linked to psychiatric traits are marked in a lighter shade of blue.

We estimated the cultural variance contained within each of these countries using three indices. One index was the *Muthukrishna index*, which measured country-specific variability of responses to the World Values Survey (Inglehart et al., 2014) using a method derived from Muthukrishna et al. (2020), which was in turn derived from the Fixation Index or F_{ST} (L. L. Cavalli-Sforza et al., 1994). The other two indices were the *Uz domain-general* and *Uz domain-specific indices*, which were both designed by Uz (2015) to be proxies of cultural tightness/looseness—a construct that captures the strength of social norms and enforcement of behavioral homogeneity in a society (Gelfand et al., 2011; Pelto, 1968; Triandis, 1989). Whereas the domain-general index measures variability across all variables in the World Values Survey and European Values Survey, the domain-specific index is restricted to a subset of variables that probe moral judgments.

As a preliminary test, we measured Pearson's correlations between heritability estimates and cultural variance of the country in which the estimate was observed. Obtaining correlations across the 3 cultural variance indices and the 3 trait sets, we found a small but robust negative association among the culturally transmissible traits (the restricted and inclusive sets) and no association for the acultural traits, as predicted. For the inclusive set of traits, the correlation was on the order of $r = -0.1$ to -0.2 across the three indices (**Table 4.1**; **Figure 4.4**). The magnitudes of the correlations for the restricted set were within the same range as for the inclusive trait set, but the results were noisier (i.e., higher p-values) most likely due to the smaller sample sizes that occured as a result of omitting the psychiatric traits. These correlations were not driven by outliers: when all data points that fell outside of ±2 standard deviations from mean cultural variance were removed, the correlation coefficients increased rather than decreased across all 3 indices for both the inclusive and restricted sets, in some cases by more than a factor of 2 (see **Figure 4.4**).

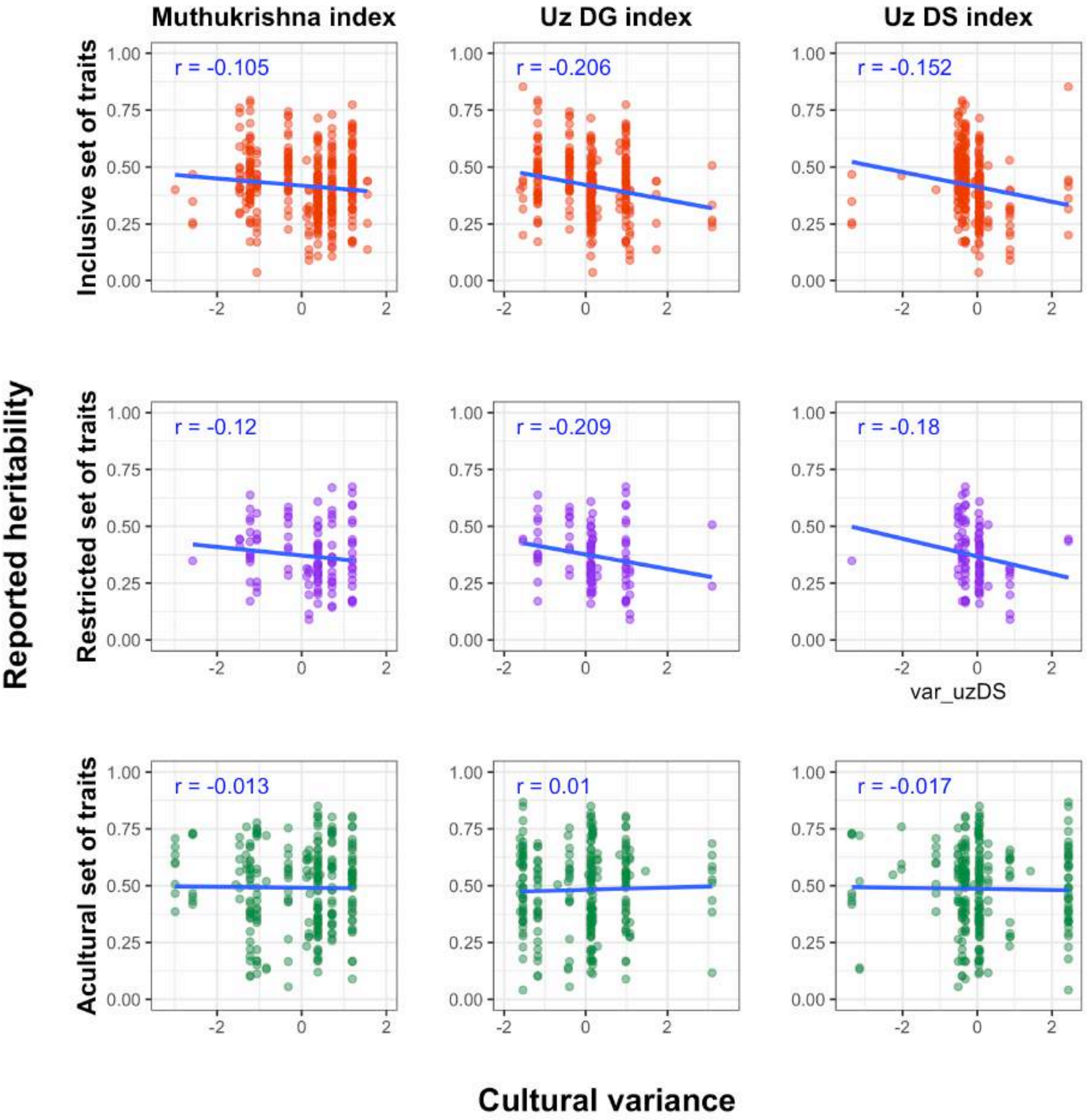

Figure 4.4: Scatterplots displaying all observations across the 9 combinations of cultural variance index and trait set, visualizing the relationship between cultural variance and reported heritability for each. Linear trend lines and Pearson's correlation coefficients are displayed for each panel. See Table 4.1 for details of these analyses.

We then conducted a specification curve analysis across 30 mixed-effects models configured according to different specifications, all of which were preregistered. Configured variables included the choice of cultural variance index (among the 3 described above); whether the phenotypic traits were specified at the level of broad ("domains") or fine-grained (ICF/ICD10 subchapters) categories—where the mapping of studies to categories was given by Polderman et al. (2015); and the inclusion of 3 control variables: GDP per capita, years of education, and population size. Cultural variance and the control variables were entered as fixed effects, while phenotypic trait (domain or subchapter), study type (i.e., gender arrangement of the twin pairs), and country were entered as random effects with random intercepts only. The specifications of these 30 models are indicated in **Figure 4.5**, further explained in the **Methods** section, and fully described in **Table 4.9**.

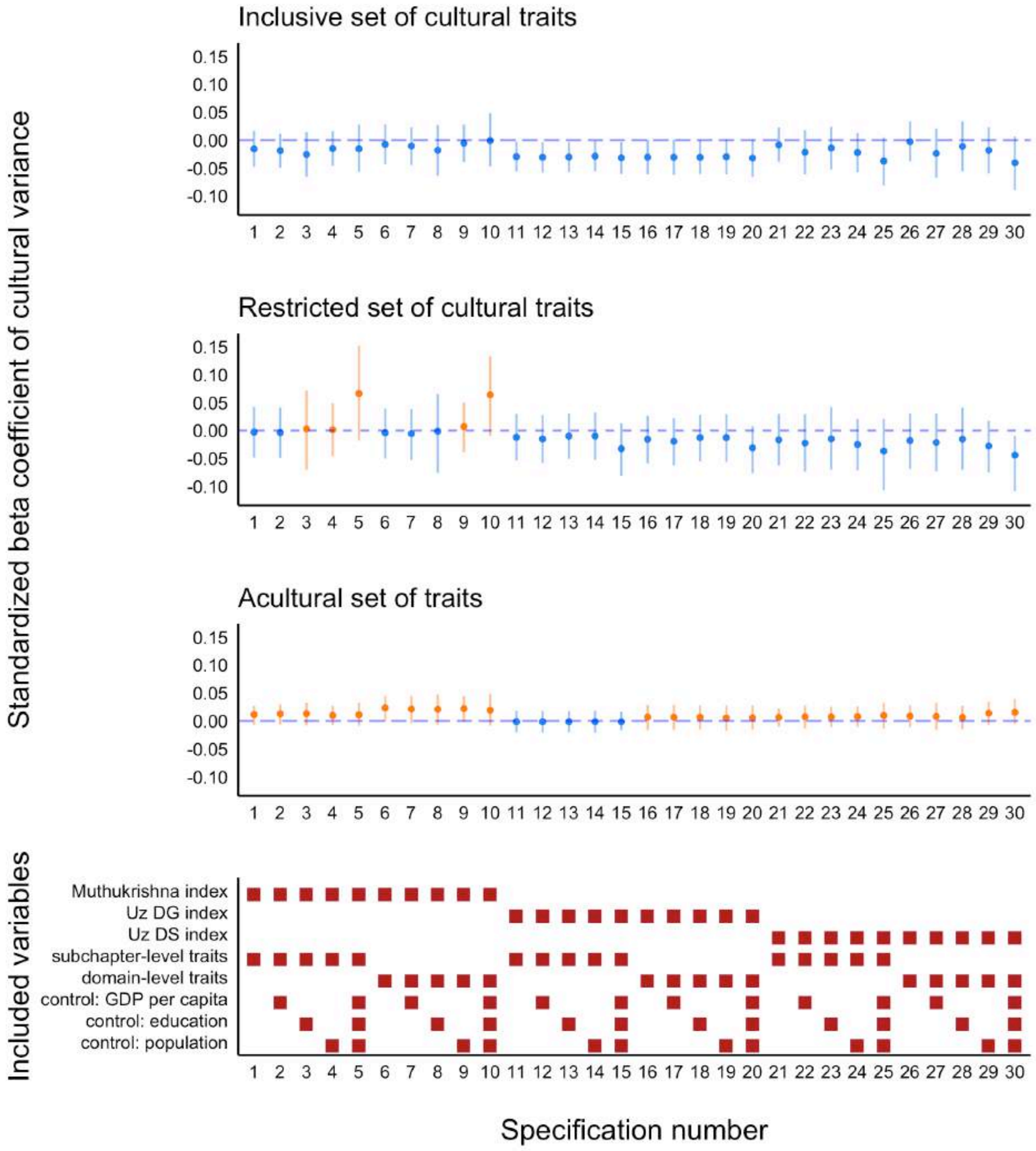

Figure 4.5: Ensemble presentation of standardized regression coefficients of cultural variance with respect to heritability across 30 model specifications, in separate panels for the inclusive, restricted, and acultural trait sets. Orange and blue points indicate positive and negative coefficient values respectively. Error bars mark 95% confidence intervals. Red boxes in the lower panel indicate the variables that were included in each model. See Methods for details, Tables 4.3–4.8 for model outcomes, and Table 4.9 for precise model specifications.

The standardized beta coefficient of cultural variance was estimated to be negative across all of the 30 models for the inclusive set of culturally transmissible traits (**Figure 4.2**), confirming our prediction of an inverse relationship between cultural variance and heritability. The mean coefficient value was -0.02, implying that within the scope of the present data set, a 1 standard deviation increase in cultural variance is associated with a 2% drop in the heritability of culturally transmissible traits. Statistical significance for the slope (at $p<0.05$) was reached in only 3 out of the 30 model specifications (i.e., specifications 11, 12, and 13), but as noted in our preregistration, we had disregarded the use of statistical significance as our criterion for success. This decision was due to the expectation of noisy data as well as a pronounced restriction of range in cultural variance for countries with available data (**Figure 4.7**).

For the restricted set of culturally transmissible traits, the standardized beta coefficient of cultural variance was estimated to be negative as predicted in 25 of the 30 models and positive in the remaining 5 (**Figure 4.2**), thus supporting the relationship we had predicted but with somewhat less certainty compared to the inclusive set. The mean coefficient value was -0.01, implying that within the scope of the present data set, a 1-standard deviation increase in cultural variance is associated with a 1% drop in the heritability of culturally transmissible non-psychiatric traits. Beta coefficients of cultural variance did not reach statistical significance in any of the models.

For the acultural set of traits, the standardized beta coefficient of cultural variance was estimated to be positive in 25 of the 30 models and negative in the remaining 5 (**Figure 4.2**), thereby demonstrating a qualitative gap between the psychological and behavioral traits that make up the inclusive and restricted sets on the one hand, and anatomical and physiological traits that make up the actultural set on the other. The mean coefficient value was 0.009, implying that within the scope of the present data set, a 1-standard deviation increase in cultural variance is associated with a 0.9% rise in the heritability of traits that are less culturally transmissible. Beta coefficients of cultural variance did not reach statistical significance in any of the models.

As an additional test of robustness, we ran the same analysis after imputing missing cultural variance scores. Among the heritability data, some observations were not matched by a corresponding cultural variance score for the country in which the estimate was collected. Where we could, we imputed cultural variance scores to these missing countries, by averaging the scores of adjacent neighbors. The increase in the number of data points through the use of this procedure ranged from ~3% to ~20% across the 3 cultural variance indices. Although the imputation method was underspecified in our preregistration, we adopted a systematic procedure (see **Methods**). Analysis following imputation revealed virtually no difference in results from the unimputed data, further demonstrating the robustness of our results (**Figure 4.8** and **Tables 4.3–4.8, Appendix**).

The present study allowed us to infer the standardized effect size of cultural variance with respect to the heritability of culturally transmissible traits. The inclusive trait set provided an ensemble of models with relatively less noise (e.g., narrower confidence intervals) and greater consistency of outcomes compared to the restricted set, and thus a somewhat better estimate. We therefore illustrate the effect size of cultural variance in **Figure 4.6** using the models that were fitted to the inclusive set of traits. A standardized beta estimate of –0.02 suggests that the difference in heritability between countries in our sample with low cultural variance, such as Japan and China, and those with high cultural variance, such as France and Belgium, is expected to be on the order of 10% (for a trait of average heritability). Note that "average" here refers to the average heritability among published estimates in the twin study literature, which is influenced by the interests of researchers and funding bodies, and should not be construed as a distribution of phenotypes that is somehow intrinsic to the human organism.

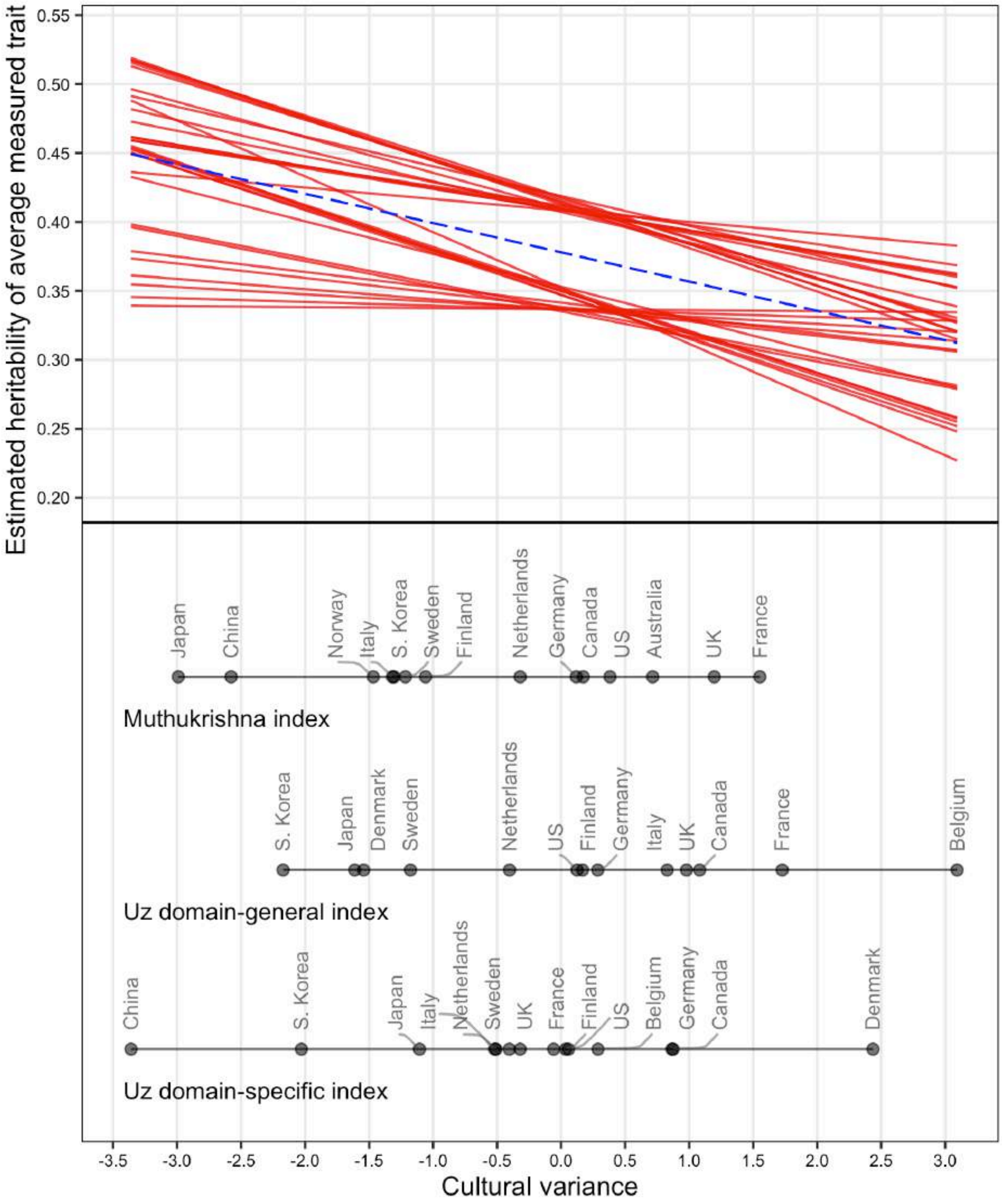

Figure 4.6: Aggregate slope of the fixed effect of cultural variance with respect to heritability for the Inclusive set of culturally transmissible traits. *Upper panel*: Each of the 30 red lines represents a linear model derived from the analysis given in the top-most panel of Figure 4.5. The blue dashed line displays the mean intercept and slope of the 30 models. Heritability scores here should be interpreted not as estimates of some intrinsic set of human traits, but rather as estimates for traits that are studied and reported in the twin study literature. *Lower panel*: Cultural variance scores of all countries whose data were used in the analysis for the inclusive set of traits, with separate scales displayed for the 3 cultural variance indices. Cultural variance scores are standardized with respect to the density of the observed data, and not to the distribution of countries.

Discussion

The results of this cross-national analysis support our prediction of a negative association between cultural variance and heritability for culturally transmissible traits. Analysis of the inclusive set of culturally transmissible traits indicated a clear directionality in the effect of cultural variance, with perfect uniformity in the sign of the beta coefficients. None of the control variables (i.e., GDP per capita, education, and population) were critical for the effect, and their inclusion did not reveal any systematic changes in the outcome, suggesting that the effect is robust (**Figure 4.5**; **Tables 4.3–4.5**).

Analysis of the restricted set of traits was less consistent but agreed with the results of the inclusive set, with the large majority of models (83%) yielding a sign in the predicted (i.e., negative) direction. The effect sizes were smaller than the inclusive set possibly due to the smaller sample size, which was 118 for the restricted set compared to 362 for the inclusive set. The resulting noise was captured by differences in the width of the 95% confidence intervals between the two sets—a mean width of 0.093 percent heritability for the restricted set compared to 0.062 for the inclusive set.

Analysis of the acultural set of traits yielded yet narrower confidence intervals (0.038) and hence a relatively small amount of noise, which helped to make plain the contrast in outcome compared to the other two analyses: the large majority of coefficients (83%) were positive for the acultural set. We are not aware of any theoretical reason for the effect to be positive as opposed to null, and further study will be required to evaluate the true form of this relationship. Imputation of missing cultural variance scores led to virtually no change in the results of any of these analyses, adding to the evidence for the robustness of our results (**Figure 4.8**; **Tables 4.6–4.8**).

The phenotypic traits used in this study were sorted into the 3 sets based on our subjective judgments about which traits were likely to be culturally transmissible and which were not, with these choices being preregistered. Despite the inevitable noise introduced by this suboptimal hand-picking procedure, a qualitative difference in results was nonetheless found between the inclusive and restricted sets on the one hand and the acultural set on the other, with a divergence in directionality that confirmed our hypothesis. Analyses of the models were mostly not statistically significant, but in our preregistration we had disregarded statistical significance as our criterion for success. According to the standards that we did adopt, the present outcome serves as evidence that heritability and cultural variance are negatively associated through the mediation of cultural transmissibility. By preregistering the hypotheses, the allocation of traits into the 3 sets, and the model specifications, we reduced the likelihood of a researcher-induced false-positive and strengthened replicability. If it were possible to employ a more systematic method for the selection of culturally transmissible traits in place of hand-picking, the size of the effect would likely be less attenuated by the noise introduced by our procedure, and thus larger.

Our analysis was limited by a restriction of range in the available data, as they were drawn from historical published data which are heavily skewed toward a small number of Western countries (a problem that also persists in GWAS; see Need & Goldstein, 2009; Popejoy & Fullerton, 2016; Sirugo et al., 2019). Of the 362 heritability estimates that were linked to the inclusive set of traits, 203 (56%) were from the US, UK, or Australia, and only 8 (2%) were from non-Western countries (Polderman et al., 2015b). Similarly for the restricted set of traits, 72 (61%) of the 118 estimates were from US, UK, or Australia, and only 1 (0.8%) was from a non-Western country. Because the countries that were heavily represented in these data occupy a narrow range of cultural variance relative to the global distribution (see densities of red ticks in **Figure 4.7**), our method of standardizing cultural variance with respect to extant data produces estimates that are intrinsically misleading unless this restriction of range is accounted for. If the effect found in the present study is valid and can be extrapolated beyond the range of the extant data, then more globally representative sampling of heritability estimates, if achievable, would require us to recalibrate the scale of cultural variance such that 1 standard deviation would contain a greater absolute range of cultural variance. This would increase the standardized effect beyond the estimate we obtained from the extant data, and the slope of the effect depicted in **Figure 4.6** would presumably become steeper as the data become less skewed and more balanced.

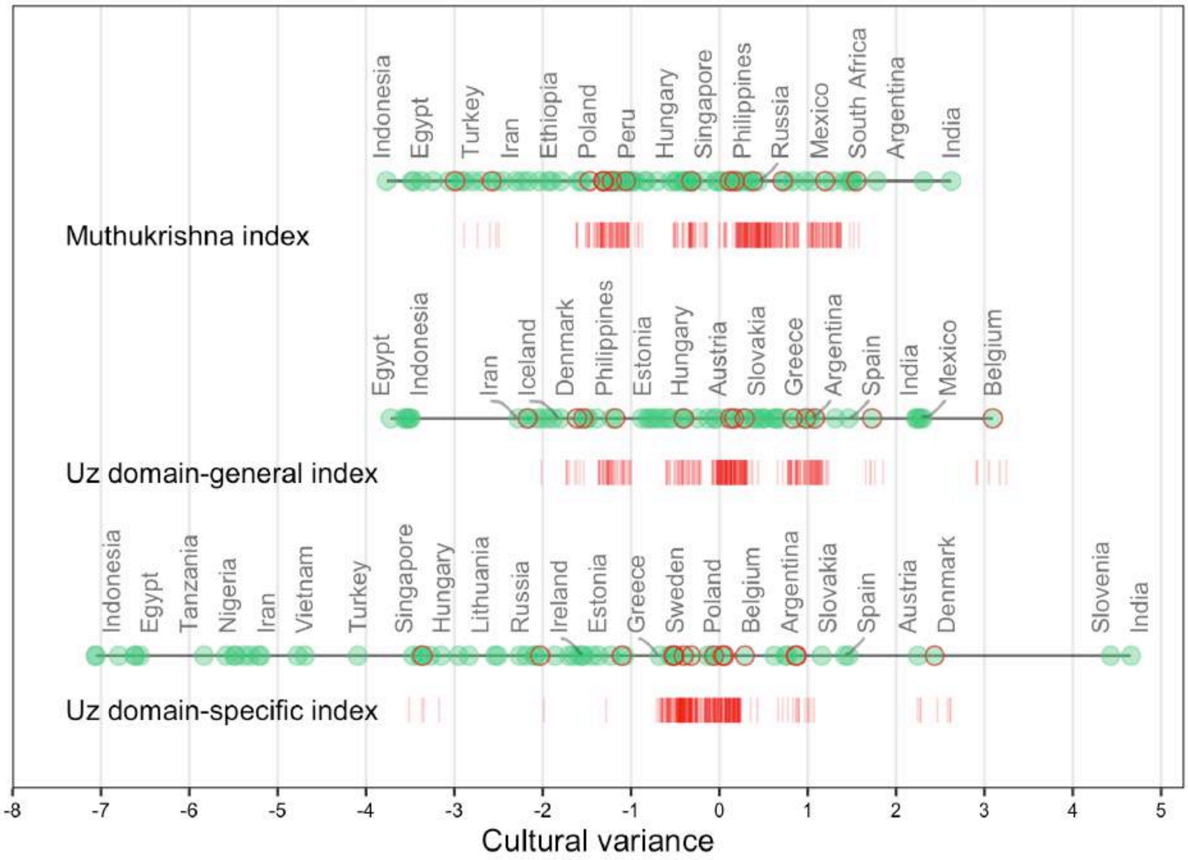

Figure 4.7: Green points indicate cultural variance scores of all countries for which scores were available, including the many countries that do not appear in the present study due to the absence of corresponding heritability estimates. Separate scales are displayed for each of the 3 cultural variance indices, and country names are labeled for a subset of the countries. Red circles indicate countries whose data were used in the analysis of the inclusive set of traits, and thus coincide with the grey points in the lower panel of Figure 4.6. Arrays of red ticks represent all of the observations linked to the inclusive set of traits, and are jittered horizontally to facilitate the visualization of density. Cultural variance on the horizontal axis is standardized with respect to the distribution of observations (with exactly the same scale as in Figure 4.6 but an expanded range due to the inclusion of more countries), and not the distribution of countries.

In addition to the above limitations, the use of country as a unit of analysis brings its own limitations as well. Fundamentally, our target of interest is not the particular heritabilities of extant countries, as estimation of cultural variance at the level of countries is necessarily a coarse abstraction whose quantity could be explained by multiple possible underlying causes. One possible explanation for a given cultural variance score is cultural tightness/looseness (Gelfand, 2018; Gelfand et al., 2006, 2011b), where "tight" societies favor adherence to social norms while "loose" societies tend to tolerate deviant behavior. Another possible explanation is the dynamics of innovation and diffusion (see also Muthukrishna & Henrich, 2016)—while loose societies are associated with increased innovation and tighter societies are associated with more extensive diffusion, tightness/looseness can also vary independently of innovation and diffusion. In Uchiyama et al. (forthcoming), we present a formal model of how the dynamics of innovation and diffusion are expected to shape cultural variance and thus heritability. Finally, cultural variance may be explained by the clustering of sub-groups within a population, or "cultural clustering" (Muthukrishna et al., 2020a; Uchiyama et al., forthcoming). Cultural clustering can in turn be explained by multiple underlying causes of its own, including various barriers (e.g., geographic, linguistic, caste) that impede cultural interaction, large-scale immigration, or the drawing of administrative boundaries that do not respect the geographic arrangement of cultural groups, as occurs often under colonial administration (e.g., Michalopoulos and Papaioannou 2020). Such factors may be co-present in different mixtures across the geographic span of a country, resulting in an inverse problem that obstructs inference of the underlying causes. This remains a problem if cultural variance is measured on the scale of gross units of organization such as country.

A more meaningful target of interest is a general understanding of how variation within the space of possible forms of cultural organization controls heritability, and how this relationship can help us recover the true structure of the inputs (genetic, ecological, cultural) that explain phenotypic development and variation. Instead of just measuring the aggregate variation observed within the span of a country's borders, a more appropriate measure would at least capture the cultural variance experienced by the average individual, analogous to the difference between standard measures of population density and *population-weighted* density, which measures the density at which the average person lives (S. G. Wilson et al., 2012). Due to these problems associated with the use of country as a unit of analysis, even if we were able to overcome the restriction of range in the present data and collect samples uniformly across the full set of countries labelled in **Figure 4.7**, the resulting data would remain limited in their ability to capture the true relationship between cultural variance and heritability.

If heritability of culturally transmissible traits is mediated by differences in cultural variance across populations as our results suggest, then this heritability should also be mediated by differences in cultural variance across time within a single population. A cultural evolutionary approach predicts that the variability of cultural traits within a society is shaped not only by slowly changing factors such as linguistic or religious clustering, but also by more rapidly changing factors including technological innovations, in domains such as communication and transportation, and social innovations, such as the diffusion of norms and values that influence the dynamics of cultural transmission (e.g., cultural change from collectivism to individualism; Hamamura, 2012; Mesoudi et al., 2016). Such innovations, whether technological or social, reconfigure the network structure of cultural transmission and drive changes in cultural variance over fast time scales. The proliferation of social media is an interesting example, which can potentially boost or inhibit cultural variance depending on a combination of factors both intrinsic (e.g., design of the social media algorithm) and extrinsic (e.g., real-world political context) to the medium of communication (Allcott et al., 2020; Asimovic et al., 2021; Bail et al., 2018; Urman, 2020). Contemporary estimates of the heritability of psychological and behavioral traits are thus likely to be limited in their generalizability across time, and the extent of this limitation will depend upon factors such as the rate of innovation and depth of cultural change (Henrich, 2004a; Muthukrishna & Henrich, 2016a). In addition to its role in shaping the distribution of the environmental variance component that we have focused on in the present study, cultural evolution commonly also masks or unmasks genetic effects by producing cultural adaptations that functionally overlap with gene function, further hindering the generalizability of genetic effects across societies and across time (Uchiyama et al., forthcoming).

Due to these various limitations, the results of the present study should not be construed as an estimation of the true effect of cultural variance. The results do however serve as a signal of how the malleability of the heritability statistic may be coupled to cultural evolution. That heritability is dependent on environmental conditions is already well understood in behavioral genetic research (e.g., Charmantier & Garant, 2005; Feldman & Ramachandran, 2018; Haworth & Davis, 2014; Lewontin, 1970; Moore & Shenk, 2016; Tenesa & Haley, 2013; Vitzthum, 2003), but the systematic ways in which cultural dynamics shape the environmental component of phenotypic variation is a topic that has not received sufficient attention (Uchiyama et al., forthcoming). A cultural evolutionary approach to behavioral genetics can provide leverage for predicting how changes in culture, including through interventions in domains such as education or therapy, can lead to changes in genetic effects. It also offers a more realistic picture of human phenotypic development, for example highlighting how the generalization of genetic effects from other species to our own requires caution due to the complex but often veiled effects of cumulative culture. A deeper understanding of the formation of our psychological and behavioral phenotypes requires closer integration with the theoretical framework of cultural evolution.

Methods

Preregistration

An initial preregistration as well as a subsequent addendum were uploaded to the Open Science Framework. These documents are available at the following URL: https://osf.io/brdct

Data

In order to gather heritability estimates across a mix of various phenotypic domains while reducing bias involved in the selection of traits, we drew upon a comprehensive meta-analysis that lays claim to covering virtually all twin studies published between 1958 and 2012 (Polderman et al., 2015b). Using the MaTCH web-tool (https://match.ctglab.nl) that was developed by the authors of the meta-analysis, we obtained mean within-country heritability estimates for all traits in the data set. The MaTCH data set gives separate heritability estimates for four study types: those assessing male twins only (*h2_m*), female twins only (*h2_f*), twins that are same-sex but whose sex is unreported (*h2_ss*), and twins in which sex is either mixed or unknown (*h2_all*). We retained for our analysis all data points in which at least one heritability estimate under the full ACE or ADE model was available across any of the above four study types.

We then sorted these data points into three groups, each corresponding to a set of phenotypic traits. Two of these sets consisted of traits that we had judged likely to be culturally transmissible, after examining their definition or operationalization in the original papers that were identified in the Polderman et al. (2015) meta-analysis. We pre-registered these two trait sets prior to conducting the analysis. One set is the *restricted* set of culturally transmissible traits, whose entries broadly fall under the umbrella of psychological and behavioral traits, containing

118 observations distributed across 18 traits and 10 countries (**Figure 4.1**; see **figure 4.3** for the distribution of observations across countries). The other set was the *inclusive* set of culturally transmissible traits, which consists of the Restricted list combined with psychiatric traits, containing 362 observations distributed across 50 traits and 14 countries (**Figure 4.2**). We had separated out the psychiatric traits from the Restricted list because we were not sure if psychiatric traits would behave in the same manner as the other non-clinical (but culturally transmissible) traits. We then gathered the remaining phenotypic traits into a *Acultural* set of traits, which constituted 301 observations—these were traits that we omitted from the pre-registered sets because we judged them less likely to be culturally transmissible.

Not all of these observations could be used for analysis due to missing cultural variance scores for some countries. Of the 362 observations of the inclusive set, 348 could be used for the Muthukrishna index, 288 could be used for the Uz domain-general index, and 292 could be used for the Uz domain-specific index. Of the 118 observations of the restricted set, 114 could be used for the Muthukrishna index, 95 could be used for the Uz domain-general index, and 96 could be used for the Uz domain-specific index. Of the 301 observations of the acultural set, 249 could be used for the Muthukrishna index, 251 could be used for the Uz domain-general index, and 258 could be used for the Uz domain-specific index.

Measures of Cultural variance

Muthukrishna index

This index of cultural variance is derived from the procedure that Muthukrishna et al. (2020) used to compute Cultural Distance. Cultural Distance is a between-country distance measure that summarizes patterns of variation in responses to the World Values Survey (WVS). It uses the same method as the fixation index, or F_{ST}, which is commonly employed in population genetics to measure genetic differentiation between groups of organisms (Cavalli-Sforza et al., 1994). Instead of comparing the variation in WVS responses between pairs of countries as Cultural Distance does, we extracted the variation present *within* countries. Muthukrishna et al. (2020) collapsed graded responses to WVS questions into 2 or 3 categorical responses that code the valence of the original response (e.g., coarsening a 9-point

Likert scale into "positive", "neutral" or "negative" responses), in order to mitigate the impact that cross-cultural variation in response style may have on the analysis. However, this procedure also reduces the amount of potentially meaningful variation in the data, and we observed that the collapsed responses were inadequate for computing variability and comparing this quantity across societies. We therefore decided to use the raw, pre-collapsed WVS responses, and indicated this in a subsequently registered addendum to our original preregistration.

To compute cultural variance, we started with the same 145 WVS questions as selected by Muthukrishna et al. (2020), and after dropping all questions that we judged to be nominal variables, as well as all missing or invalid survey responses (i.e., those coded as negative numbers in WVS), we used Min-Max scaling to normalize all remaining ordinal and interval variables such that the range of possible responses for each question was bound between 0 and 1. For each country, we computed the within-country variance for each of these normalized variables and took their average to obtain a country-specific cultural variance score: the higher the score, the more diverse the WVS responses from that country. Ordinal variables make up the majority of the WVS questions that we use for the Muthukrishna index, and we recognize the methodological problems associated with conducting statistical procedures on ordinal variables as if they were metric (Liddell & Kruschke, 2018)—in the present case, the computation of variance in particular. However, we believe that the procedure is justified because the purpose of our analysis is not to infer the population distributions that generated the data but rather to estimate relative differences in variance across countries.

Uz indices

Prior to Muthukrishna et al. (under review), Uz (2015) had constructed a similar measure that was intended to be an index of Cultural Tightness–Looseness (CTL; Gelfand et al., 2011; Pelto, 1968; Triandis, 1989). CTL is postulated to be a population-level trait that captures the strength of social norms and resistance to deviant behaviour in a society. Uz (2015) uses the within-country standard deviation in responses to WVS and EVS questions as a proxy for CTL, where more variation in responses is assumed to reflect a Looser society. Out of the three indices created by Uz (2015), we test two: the Domain-General (DG) Index and the Domain-Specific (DS) Index, with this choice being entered in our pre-registration. The former uses all available data, whereas the latter is limited a subset of the EVS known as the Morally Debatable Behaviors Scale (Harding & Phillips, 1986), which specifically probes participants' attitudes toward morally contentious topics such as abortion, divorce, and suicide. In terms of procedure for creating the variable, The Uz DG Index is very similar in its construction to the Muthukrishna index, differing in details such as the WVS wave it uses and the criteria by which survey questions are excluded

Imputation of cultural variance scores

Among the heritability observations, some were not matched by a corresponding cultural variance score for the country in which the data were collected. This was due either to the country not being included in the WVS wave used for the Muthukrishna index, or in the case of the Uz indices, not being available in the index. We therefore ran another version of the analysis in which cultural variance scores for these missing countries were imputed by averaging the scores of their adjacent neighbors where they were available. We preregistered the intent to perform this analysis and specified some of the neighbor countries to use for imputation in an addendum to the original preregistration, but this list of neighbor countries was incomplete, identifying neighbors for only 2 of the 5 countries for which we ultimately imputed cultural variance scores. However, the selection of these 5 countries derived directly from the data, and identification of adjacent neighbors was mostly unambiguous for the non-island countries.

For the Muthukrishna index, cultural variance scores were missing for Belgium, Denmark, Israel, and Sri Lanka. For the Uz domain-general index, cultural variance scores were missing for Australia, Brazil, China, Gambia, Israel, Norway, and Sri Lanka. For the Uz domain-specific index, cultural variance scores were missing for Australia, Brazil, Gambia, Israel, Norway, Sri Lanka. The identification of adjacent countries was clear for most countries, but less so for the island countries of Australia and Sri Lanka, and separation by water weakened the assumption of cultural contiguity, so we omitted these two countries from this analysis. Gambia was also omitted as cultural variance scores for its sole adjacent neighbor, Senegal, were not available.

For the included countries, we identified the following neighbors:

- **Belgium**: France*, Germany*, Netherlands*, and Luxembourg
- **Brazil**: French Guinea, Suriname, Guyana, Venezuela*, Colombia, Peru*, Bolivia, Paraguay, Argentina*, Uruguay
- **China**: Russia*, Mongolia, North Korea, Kazakhstan, Kyrgyzstan*, Tajikistan, Afghanistan, Pakistan*, India*, Bhutan, Burma, Nepal, Laos, and Vietnam*
- **Denmark**: Sweden* and Germany*
- **Israel**: Jordan*, Lebanon*, Syria, and Egypt
- **Norway**: Sweden* and Finland*

Cultural variance scores were not available for all neighbor countries; neighbor countries for which a score was available for use in imputation (for any of the cultural variance indices) are marked above with an asterisk. Not all neighbor country scores were available for all cultural variance indices—specific neighbors used in imputation of missing country scores for each index are listed in **Table 4.2**.

We took the arithmetic mean of the scores of the available neighbor countries to impute a cultural variance score for each target country. For the inclusive set of traits, imputation of cultural variance increased the number of usable observations from 348 to 361 for the Muthukrishna index, from 288 to 308 for the Uz domain-general index, and from 292 to 308 for the Uz domain-specific index. For the restricted set of traits, imputation of cultural variance increased the number of usable observations from 114 to 118 for the Muthukrishna index, from 95 to 99 for the Uz domain-general index, and from 96 to 99 for the Uz domain-specific index. For the acultural set of traits, imputation of cultural variance increased the number of usable observations from 249 to 300 for the Muthukrishna index, from 251 to 265 for the Uz domain-general index, and from 258 to 265 for the Uz domain-specific index.

Analysis

For our main analysis we fitted linear mixed effects models to our data using the *lme4* package (D. Bates et al., 2015) in the R programming language. The Muthukrishna and Uz indices of cultural variance were our main predictors of heritability, our outcome variable. To control for possible confounds of cultural variance, we included the following control variables as fixed effects: GDP per capita, mean years of education, and population size, each taken from the Varieties of Democracy (V-Dem) Version 9 data set (Coppedge et al., 2019). We used the 2006 values for these controls, as this was the median year of all of the studies included in the meta-analysis of Polderman et al. (2015).

We included several random effects to account for non-independence among data points. One of these was the phenotypic trait itself. In addition to the different trait-lists described above, we also varied the level of granularity at which phenotypic traits are specified: Polderman et al. (2015) adopted a three-tiered system for the classification of phenotypic traits, and we included in our analyses either the traits specified at the most fine-grained "subchapter" level (referring to ICF/ICD10 subchapters) or at the most coarse-grained "domain" level. For example, "Memory functions" and "Global psychosocial functions" are both examples of subchapter-level traits that belong to the "Cognitive" domain. Another random effect was twin study type (*h2_m, h2_f, h2_ss, h2_all*) as noted above in the sub-section on Data. The final random effect was country.

The sources of variation in our model specifications can be enumerated as follows:

- 3 sets of phenotypic traits (inclusive; restricted; acultural)
- 3 measures of cultural variance (Muthukrishna index; Uz domain-general index; Uz domain-specific index)
- 2 levels of granularity for phenotypic traits (subchapter and domain)
- 5 configurations of control variables (GDP per capita; education; population; all three; none)

These variables combined into 30 models per set of traits (see **Figure 4.5** and **Table 4.9**). All predictors were standardized.

Appendix

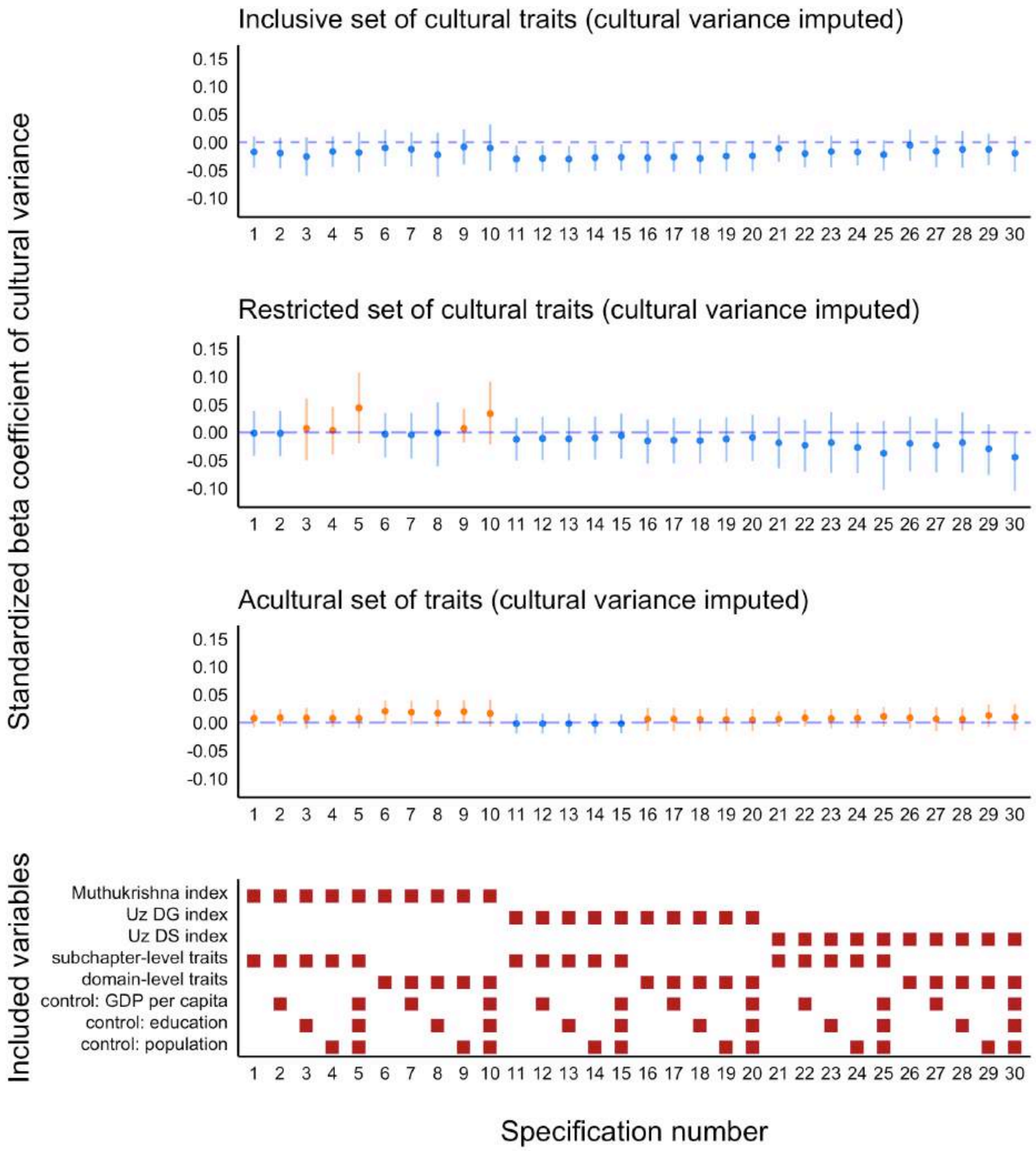

Figure 4.8: Ensemble presentation of standardized regression coefficients of cultural variance with respect to heritability across 30 model specifications, where cultural variance for missing countries has been imputed by averaging scores from adjacent neighbors. Results are displayed in separate panels for the inclusive, restricted, and

acultural trait sets. Orange and blue points indicate positive and negative coefficient values respectively. Error bars mark 95% confidence intervals. Red boxes in the lower panel indicate the variables that were included in each model. See Methods for details, Tables 4.3–4.8 for model outcomes, and Table 4.9 for precise model specifications.

Table 4.1: Results of the correlation analyses described in the Results section and illustrated in Figure 4.4.

Trait set	**Index**	***r***	**df**	***p***
Inclusive Set	Muthukrishna	−0.11	346	0.05
	Uz Domain-general	−0.21	286	<0.001
	Uz Domain-specific	−0.15	290	<0.01
Restricted Set	Muthukrishna	−0.12	112	0.20
	Uz Domain-general	−0.21	93	0.04
	Uz Domain-specific	−0.18	94	0.08
Acultural Set	Muthukrishna	−0.01	247	0.83
	Uz Domain-general	0.01	249	0.88
	Uz Domain-specific	−0.02	256	0.79

Table 4.2: Neighbor countries used in imputation of missing cultural variance scores for each cultural variance index.

Cultural variance index	Missing score	Averaged neighbors
Muthukrishna	Belgium	France
		Germany
		Netherlands
	Denmark	Sweden
		Germany
	Israel	Jordan
		Lebanon
Uz domain-general	Norway	Sweden
		Finland
	Israel	Jordan
	China	India
		Kyrgyzstan
		Russia
		Vietnam
		Pakistan
	Brazil	Argentina
		Peru
Uz domain-specific	Norway	Sweden
		Finland
	Israel	Jordan
	Brazil	Argentina
		Peru
		Venezuela

Table 4.3: Model outcomes across all 30 specifications for the inclusive set of phenotypic traits (see Figure 4.5). Marginal R^2 describes the proportion of variance explained by the fixed effects, and conditional R^2 describes the proportion of variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013).

Inclusive set of traits

Specification number	β	Lower limit 95% CI	Upper limit 95% CI	p	Marginal R2	Conditional R2
1	-0.016	-0.048	0.016	0.349	0.009	0.606
2	-0.019	-0.049	0.012	0.263	0.027	0.608
3	-0.026	-0.066	0.014	0.234	0.012	0.609
4	-0.015	-0.046	0.016	0.37	0.035	0.615
5	-0.016	-0.057	0.028	0.513	0.03	0.62
6	-0.007	-0.043	0.028	0.686	0.002	0.42
7	-0.01	-0.044	0.023	0.56	0.021	0.423
8	-0.018	-0.063	0.027	0.451	0.005	0.427
9	-0.005	-0.039	0.028	0.764	0.038	0.434
10	-0.001	-0.047	0.048	0.977	0.031	0.438
11	-0.03	-0.056	-0.003	0.045	0.031	0.571
12	-0.031	-0.058	-0.003	0.049	0.033	0.576
13	-0.03	-0.057	-0.004	0.047	0.052	0.582
14	-0.029	-0.056	-0.001	0.063	0.036	0.579
15	-0.032	-0.06	-0.003	0.069	0.048	0.594
16	-0.03	-0.061	0.001	0.066	0.028	0.415
17	-0.031	-0.062	0.001	0.081	0.027	0.425
18	-0.031	-0.061	-0.001	0.071	0.048	0.431
19	-0.03	-0.061	0.002	0.089	0.029	0.426
20	-0.032	-0.066	0.001	0.102	0.049	0.45
21	-0.008	-0.039	0.023	0.6	0.001	0.574
22	-0.022	-0.061	0.018	0.319	0.014	0.58
23	-0.014	-0.053	0.025	0.497	0.004	0.581
24	-0.022	-0.057	0.013	0.255	0.042	0.585
25	-0.037	-0.081	0.005	0.162	0.034	0.587
26	-0.003	-0.038	0.034	0.882	0	0.437
27	-0.024	-0.068	0.021	0.321	0.027	0.445
28	-0.011	-0.056	0.034	0.637	0.005	0.448
29	-0.018	-0.059	0.023	0.413	0.04	0.452
30	-0.04	-0.089	0.007	0.164	0.039	0.446
mean	-0.021					

Table 4.4: Model outcomes across all 30 specifications for the restricted set of phenotypic traits (see Figure 4.5). Marginal R^2 describes the proportion of variance explained by the fixed effects, and conditional R^2 describes the proportion of variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013).

Restricted set of traits

Specification number	β	Lower limit 95% CI	Upper limit 95% CI	p	Marginal R^2	Conditional R^2
1	-0.003	-0.048	0.042	0.905	0	0.61
2	-0.004	-0.049	0.041	0.881	0.006	0.617
3	0.003	-0.07	0.071	0.938	0.001	0.613
4	0.001	-0.046	0.049	0.954	0.007	0.617
5	0.066	-0.018	0.152	0.274	0.039	0.62
6	-0.004	-0.05	0.039	0.869	0	0.414
7	-0.005	-0.053	0.039	0.826	0.008	0.432
8	-0.001	-0.076	0.066	0.973	0.001	0.423
9	0.007	-0.039	0.05	0.774	0.027	0.432
10	0.064	-0.009	0.133	0.28	0.056	0.448
11	-0.012	-0.054	0.03	0.579	0.005	0.571
12	-0.015	-0.058	0.028	0.535	0.014	0.591
13	-0.01	-0.051	0.03	0.658	0.036	0.587
14	-0.01	-0.052	0.032	0.676	0.013	0.59
15	-0.032	-0.081	0.013	0.348	0.052	0.603
16	-0.016	-0.059	0.026	0.476	0.008	0.459
17	-0.019	-0.062	0.022	0.427	0.02	0.487
18	-0.013	-0.055	0.029	0.582	0.038	0.468
19	-0.012	-0.056	0.03	0.599	0.02	0.483
20	-0.031	-0.076	0.008	0.386	0.048	0.502
21	-0.017	-0.063	0.03	0.451	0.005	0.559
22	-0.022	-0.074	0.03	0.411	0.01	0.574
23	-0.015	-0.07	0.041	0.609	0.004	0.572
24	-0.025	-0.072	0.021	0.324	0.037	0.576
25	-0.037	-0.107	0.021	0.351	0.036	0.596
26	-0.018	-0.069	0.031	0.429	0.005	0.445
27	-0.021	-0.073	0.031	0.434	0.008	0.468
28	-0.015	-0.071	0.041	0.593	0.004	0.466
29	-0.028	-0.075	0.018	0.273	0.045	0.468
30	-0.044	-0.109	-0.009	0.248	0.045	0.485
mean	-0.01					

Table 4.5: Model outcomes across all 30 specifications for the acultural set of phenotypic traits (see Figure 4.5). Marginal R^2 describes the proportion of variance explained by the fixed effects, and conditional R^2 describes the proportion of variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013).

Acultural set of traits

Specification number	β	Lower limit 95% CI	Upper limit 95% CI	p	Marginal R^2	Conditional R^2
1	0.011	-0.007	0.027	0.154	0.005	0.6
2	0.013	-0.006	0.029	0.128	0.005	0.6
3	0.013	-0.008	0.033	0.276	0.004	0.601
4	0.01	-0.008	0.027	0.349	0.004	0.608
5	0.011	-0.009	0.033	0.431	0.004	0.617
6	0.023	-0.001	0.045	0.064	0.019	0.387
7	0.021	-0.004	0.045	0.107	0.018	0.391
8	0.021	-0.007	0.047	0.148	0.019	0.39
9	0.022	-0.002	0.045	0.092	0.019	0.391
10	0.019	-0.008	0.048	0.238	0.02	0.401
11	-0.001	-0.021	0.018	0.897	0	0.573
12	-0.001	-0.021	0.018	0.899	0.001	0.577
13	-0.001	-0.02	0.018	0.902	0	0.573
14	-0.001	-0.021	0.018	0.91	0	0.577
15	-0.001	-0.017	0.016	0.911	0.001	0.587
16	0.007	-0.016	0.029	0.547	0.002	0.37
17	0.007	-0.016	0.029	0.575	0.003	0.376
18	0.007	-0.015	0.028	0.562	0.006	0.373
19	0.005	-0.018	0.028	0.666	0.005	0.377
20	0.006	-0.016	0.028	0.66	0.006	0.382
21	0.006	-0.01	0.022	0.452	0.002	0.579
22	0.007	-0.013	0.028	0.519	0.002	0.581
23	0.007	-0.011	0.026	0.485	0.002	0.583
24	0.008	-0.011	0.026	0.451	0.002	0.581
25	0.01	-0.013	0.033	0.533	0.003	0.591
26	0.009	-0.011	0.028	0.387	0.003	0.37
27	0.008	-0.016	0.032	0.532	0.003	0.374
28	0.006	-0.015	0.027	0.568	0.004	0.373
29	0.014	-0.007	0.035	0.23	0.008	0.373
30	0.015	-0.005	0.039	0.321	0.009	0.372
mean	-0.010					

Table 4.6: Model outcomes across all 30 specifications for the inclusive set of phenotypic traits with missing cultural variance scores imputed (see Figure 4.8). Marginal R^2 describes the proportion of variance explained by the fixed effects, and conditional R^2 describes the proportion of variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013).

Inclusive set of traits (cultural variance imputed)

Specification number	β	Lower limit 95% CI	Upper limit 95% CI	p	Marginal R2	Conditional R2
1	-0.017	-0.046	0.011	0.241	0.012	0.6
2	-0.019	-0.047	0.008	0.189	0.025	0.601
3	-0.026	-0.06	0.008	0.159	0.014	0.601
4	-0.017	-0.044	0.011	0.264	0.036	0.609
5	-0.018	-0.054	0.018	0.354	0.031	0.611
6	-0.01	-0.043	0.022	0.544	0.004	0.402
7	-0.013	-0.044	0.018	0.441	0.024	0.405
8	-0.022	-0.062	0.017	0.281	0.009	0.406
9	-0.008	-0.04	0.023	0.619	0.032	0.415
10	-0.01	-0.051	0.032	0.653	0.027	0.418
11	-0.03	-0.054	-0.006	0.021	0.033	0.563
12	-0.029	-0.052	-0.006	0.025	0.045	0.567
13	-0.03	-0.054	-0.006	0.024	0.031	0.566
14	-0.028	-0.051	-0.004	0.035	0.054	0.572
15	-0.027	-0.05	-0.003	0.05	0.059	0.58
16	-0.028	-0.056	0	0.056	0.025	0.407
17	-0.027	-0.054	0	0.066	0.042	0.415
18	-0.029	-0.057	-0.001	0.053	0.023	0.413
19	-0.025	-0.053	0.003	0.092	0.048	0.422
20	-0.025	-0.052	0.003	0.113	0.047	0.431
21	-0.011	-0.035	0.013	0.375	0.003	0.574
22	-0.02	-0.045	0.004	0.126	0.027	0.572
23	-0.017	-0.045	0.012	0.272	0.007	0.579
24	-0.018	-0.041	0.006	0.162	0.049	0.579
25	-0.022	-0.05	0.004	0.137	0.037	0.576
26	-0.005	-0.033	0.022	0.699	0.001	0.426
27	-0.016	-0.045	0.012	0.276	0.027	0.426
28	-0.013	-0.046	0.02	0.45	0.007	0.437
29	-0.013	-0.041	0.015	0.375	0.042	0.435
30	-0.02	-0.053	0.011	0.25	0.032	0.432
mean	-0.02					

Table 4.7: Model outcomes across all 30 specifications for the restricted set of phenotypic traits with missing cultural variance scores imputed (see Figure 4.8). Marginal R^2 describes the proportion of variance explained by the fixed effects, and conditional R^2 describes the proportion of variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013).

Restricted set of traits (cultural variance imputed)

Specification number	β	Lower limit 95% CI	Upper limit 95% CI	p	Marginal R^2	Conditional R^2
1	-0.001	-0.042	0.039	0.944	0	0.597
2	-0.002	-0.043	0.038	0.936	0.005	0.603
3	0.007	-0.05	0.061	0.814	0.002	0.598
4	0.004	-0.039	0.046	0.874	0.009	0.603
5	0.044	-0.019	0.107	0.261	0.027	0.604
6	-0.003	-0.045	0.035	0.881	0	0.41
7	-0.004	-0.047	0.035	0.843	0.007	0.426
8	-0.001	-0.06	0.054	0.976	0	0.416
9	0.007	-0.018	0.042	0.752	0.022	0.423
10	0.034	-0.022	0.091	0.386	0.032	0.425
11	-0.012	-0.051	0.026	0.536	0.006	0.569
12	-0.011	-0.05	0.028	0.605	0.008	0.578
13	-0.011	-0.05	0.027	0.574	0.007	0.573
14	-0.01	-0.049	0.029	0.634	0.021	0.582
15	-0.006	-0.047	0.034	0.791	0.025	0.6
16	-0.015	-0.056	0.023	0.453	0.008	0.461
17	-0.014	-0.055	0.026	0.511	0.01	0.472
18	-0.015	-0.056	0.024	0.487	0.009	0.467
19	-0.012	-0.052	0.027	0.581	0.029	0.479
20	-0.009	-0.051	0.032	0.705	0.032	0.495
21	-0.019	-0.064	0.028	0.395	0.006	0.561
22	-0.023	-0.07	0.023	0.329	0.013	0.569
23	-0.018	-0.073	0.037	0.517	0.005	0.572
24	-0.027	-0.073	0.018	0.266	0.043	0.576
25	-0.037	-0.103	0.021	0.31	0.04	0.588
26	-0.02	-0.07	0.028	0.377	0.006	0.449
27	-0.023	-0.072	0.025	0.349	0.011	0.459
28	-0.018	-0.072	0.036	0.514	0.005	0.469
29	-0.029	-0.076	0.015	0.23	0.05	0.468
30	-0.044	-0.104	-0.002	0.213	0.05	0.481
mean	-0.01					

Table 4.8: Model outcomes across all 30 specifications for the acultural set of phenotypic traits with missing cultural variance scores imputed (see Figure 4.8). Marginal R^2 describes the proportion of variance explained by the fixed effects, and conditional R^2 describes the proportion of variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013).

Acultural set of traits (cultural variance imputed)

Specification number	β	Lower limit 95% CI	Upper limit 95% CI	p	Marginal R^2	Conditional R^2
1	0.008	-0.009	0.023	0.308	0.002	0.601
2	0.009	-0.007	0.024	0.349	0.002	0.601
3	0.008	-0.01	0.026	0.415	0.002	0.602
4	0.007	-0.008	0.023	0.415	0.002	0.604
5	0.008	-0.01	0.026	0.511	0.002	0.609
6	0.02	-0.001	0.04	0.065	0.013	0.387
7	0.019	-0.004	0.039	0.106	0.013	0.39
8	0.017	-0.007	0.04	0.166	0.014	0.389
9	0.02	-0.001	0.04	0.084	0.012	0.389
10	0.016	-0.007	0.041	0.229	0.013	0.395
11	-0.002	-0.02	0.016	0.839	0	0.581
12	-0.002	-0.019	0.016	0.841	0	0.582
13	-0.002	-0.019	0.016	0.843	0	0.583
14	-0.002	-0.02	0.016	0.836	0	0.584
15	-0.002	-0.019	0.015	0.862	0	0.589
16	0.006	-0.016	0.026	0.563	0.001	0.379
17	0.006	-0.015	0.026	0.567	0.004	0.384
18	0.006	-0.015	0.025	0.591	0.004	0.385
19	0.005	-0.016	0.026	0.627	0.001	0.382
20	0.005	-0.016	0.026	0.679	0.005	0.391
21	0.006	-0.008	0.021	0.437	0.002	0.579
22	0.008	-0.007	0.024	0.379	0.003	0.581
23	0.007	-0.01	0.025	0.465	0.002	0.583
24	0.008	-0.01	0.025	0.43	0.002	0.582
25	0.011	-0.008	0.028	0.392	0.003	0.588
26	0.009	-0.011	0.028	0.38	0.003	0.381
27	0.006	-0.016	0.028	0.579	0.003	0.384
28	0.006	-0.014	0.026	0.577	0.004	0.384
29	0.013	-0.008	0.033	0.261	0.006	0.384
30	0.01	-0.014	0.033	0.482	0.007	0.389
mean	0.008					

Table 4.9: Precise specifications of the 30 mixed-effects models, written in the notation of the *lme4* package of the R programming language (D. Bates et al., 2015).

Specification Number	Model
1	`lmer(h2 ~ var_muth + (1|h2_type) + (1|traits_subchapter) + (1|country))`
2	`lmer(h2 ~ var_muth + gdp + (1|h2_type) + (1|traits_subchapter) + (1|country))`
3	`lmer(h2 ~ var_muth + education + (1|h2_type) + (1|traits_subchapter) + (1|country))`
4	`lmer(h2 ~ var_muth + population + (1|h2_type) + (1|traits_subchapter) + (1|country))`
5	`lmer(h2 ~ var_muth + gdp + education + population + (1|h2_type) + (1|traits_subchapter) + (1|country))`
6	`lmer(h2 ~ var_muth + (1|h2_type) + (1|traits_domain) + (1|country))`
7	`lmer(h2 ~ var_muth + gdp + (1|h2_type) + (1|traits_domain) + (1|country))`
8	`lmer(h2 ~ var_muth + education + (1|h2_type) + (1|traits_domain) + (1|country))`
9	`lmer(h2 ~ var_muth + population + (1|h2_type) + (1|traits_domain) + (1|country))`
10	`lmer(h2 ~ var_muth + gdp + education + population + (1|h2_type) + (1|traits_domain) + (1|country))`
11	`lmer(h2 ~ var_uzDG + (1|h2_type) + (1|traits_subchapter) + (1|country))`
12	`lmer(h2 ~ var_uzDG + gdp + (1|h2_type) + (1|traits_subchapter) + (1|country))`
13	`lmer(h2 ~ var_uzDG + education + (1|h2_type) + (1|traits_subchapter) + (1|country))`
14	`lmer(h2 ~ var_uzDG + population + (1|h2_type) + (1|traits_subchapter) + (1|country))`
15	`lmer(h2 ~ var_uzDG + gdp + education + population + (1|h2_type) + (1|traits_subchapter) + (1|country))`
16	`lmer(h2 ~ var_uzDG + (1|h2_type) + (1|traits_domain) + (1|country))`
17	`lmer(h2 ~ var_uzDG + gdp + (1|h2_type) + (1|traits_domain) + (1|country))`
18	`lmer(h2 ~ var_uzDG + education + (1|h2_type) + (1|traits_domain) + (1|country))`
19	`lmer(h2 ~ var_uzDG + population + (1|h2_type) + (1|traits_domain) + (1|country))`
20	`lmer(h2 ~ var_uzDG + gdp + education + population + (1|h2_type) + (1|traits_domain) + (1|country))`
21	`lmer(h2 ~ var_uzDS + (1|h2_type) + (1|traits_subchapter) + (1|country))`
22	`lmer(h2 ~ var_uzDS + gdp + (1|h2_type) + (1|traits_subchapter) + (1|country))`
23	`lmer(h2 ~ var_uzDS + education + (1|h2_type) + (1|traits_subchapter) + (1|country))`
24	`lmer(h2 ~ var_uzDS + population + (1|h2_type) + (1|traits_subchapter) + (1|country))`
25	`lmer(h2 ~ var_uzDS + gdp + education + population + (1|h2_type) + (1|traits_subchapter) + (1|country))`
26	`lmer(h2 ~ var_uzDS + (1|h2_type) + (1|traits_domain) + (1|country))`

<table>
<tr><td>27</td><td><code>lmer(h2 ~ var_uzDS + gdp + (1|h2_type) + (1|traits_domain) + (1|country))</code></td></tr>
<tr><td>28</td><td><code>lmer(h2 ~ var_uzDS + education + (1|h2_type) + (1|traits_domain) + (1|country))</code></td></tr>
<tr><td>29</td><td><code>lmer(h2 ~ var_uzDS + population + (1|h2_type) + (1|traits_domain) + (1|country))</code></td></tr>
<tr><td>30</td><td><code>lmer(h2 ~ var_uzDS + gdp + education + population + (1|h2_type) + (1|traits_domain) + (1|country))</code></td></tr>
</table>

Below:

- **Document 4.1** (pp. 137–143)

  Preregistered document following the format of aspredicted.org, uploaded to {https://osf.io/brdct} on 25 October 2019

- **Document 4.2** (pp. 144–145)

  Addendum to the initial preregistration, uploaded to {https://osf.io/brdct} on 7 November 2019

We use the pre-registration format employed by AsPredicted (https://aspredicted.org)

1) Have any data been collected for this study already?

Our study uses data only from existing data sets.

2) What's the main question being asked or hypothesis being tested in this study?
Higher degrees of cultural variance (Gelfand, Nishii & Raver, 2006) will predict, across countries, decreased heritability for culturally transmissible phenotypic traits (e.g. behavioral traits).

We suffer from small sample sizes and a restriction of range issue, the latter due to most of the relevant studies having been conducted predominantly in Western countries, and these issues may preclude us from using statistical significance as a measure of success. Nonetheless, we expect to see evidence that points in the direction of our main hypothesis, which is the negative relationship between cultural variance and heritability of culturally transmissible traits.

We intend for this study to support a broader argument about the role of culture in interpreting heritability.

3) Describe the key dependent variable(s) specifying how they will be measured.
In this study, the dependent variable will be country-specific heritability as aggregated across published studies in the 'Meta-Analysis of Twin Correlations and Heritability (MaTCH)' dataset (Polderman et al., 2015).

We intend to follow up on this study by testing heritability (or an analogous construct) as inferred from GWAS data. Here we are preregistering just the first study that employs the MaTCH dataset.

4) How many and which conditions will participants be assigned to?
We are using archival data so there are no experimental conditions.

5) Specify exactly which analyses you will conduct to examine the main question/hypothesis.
We will test a number of mixed-effects models, all with heritability as their dependent variable. We use the following predictor and controls:

Predictor (fixed effect)

1. Cultural variance as indexed by three measures:
    a. An index derived from the procedure that Muthukrishna et al. (2018) used to compute Cultural Distance, in which mean variance in cultural traits within a country is computed as part of the process of calculating cultural distance (Fst). We will use this variance within a country (var_muth)
    b. Uz's (2015) Domain-General index of Cultural Tightness–Looseness (var_uzDG)
    c. Uz's (2015) Domain-Specific index of Cultural Tightness–Looseness (var_uzDS)

Our primary measure of cultural variance is the Muthukrishna index. Since tightness–looseness is also commonly used in the literature as a similar construct, we will check these as well in the form of the two

Uz indices, but our predictions are for the Muthukrishna index. This index is calculated only on culturally transmissible traits.

Controls (random effects)

For all random effects in the model we use random intercepts only, mainly due to small sample sizes.

2. Phenotypic traits. We only include traits that we consider to be culturally transmissible. Among these, we have created two lists of traits, a list of core traits that excludes psychiatric traits and another expanded list that includes them (see below). We are less confident in the cultural transmissibility of the psychiatric traits than we are in the other selected traits, but include them in a second list as we also suspect that there may be a cultural component among at least some of these.

   In addition to the difference in scope between the two lists, we also vary the level of specification of the trait, whether it's at the ICF/ICD10 Subchapter-level in the MaTCH dataset or at the higher-order classification level of Domain. We will omit the intermediate Chapter-level due to it being rendered mostly redundant with the Domain-level by the time we get to our final list of traits.

   So we have four interchangeable variables: the core list specified at the Subchapter level (traitsA_subch), the core list specified at the Domain level (traitsA_dom), the expanded list specified at the Subchapter level (traitsB_subch), and the expanded list specified at the Domain level (traitsB_dom).
3. Study type (h2_type), i.e., between male twins (h2_m), female twins (h2_f), same-sex twins where the gender is unknown (h2_ss), and remaining pairs of twins (h2_all).
4. Country. In the Muthukrishna and Uz indices, there are a few countries for which we have heritability data but are missing cultural variance data due to the countries not being included in the surveys from which the indices are constructed. We will therefore run two versions of every model, one that excludes these countries, and another in which we roughly estimate the cultural variance scores of these countries by averaging across the scores of their immediate geographic neighbors when those neighbors' scores are known.

Controls (fixed effects)

The following variables are from the V-Dem Version 9 dataset (Coppedge et al., 2019) and are included to control for confounds with standard socio-economic variables.

5. GDP per capita (e_migdppc)
6. Years of education for citizens older than 15 (e_peaveduc)
7. National population size (e_wb_pop)

We considered including Geopolitical region (e_regionpol), within which the country variable is nested, but we omitted it due to the fact that there is only one non-Western data point (China) in the smaller set of traits listed below, and only three in the expanded list that includes psychiatric traits. (This is also part of our concern with restriction of range).

First, we will test for Pearson's correlations between heritability and cultural variance, with the latter being specified according to the three indices listed above.

We will then run a series of mixed-effects models that include various combinations of the variables listed above, to ensure robustness. Mixed-effects models are appropriate for our analyses given the non-independence of the data points (e.g., observations within the same country, for the same trait). Only random intercepts will be used.

As for the specification of the models: we will run independent models for each of the three cultural variance indices. We will similarly run independent models for the four configurations of the trait variable. Country will be included in every model as a random effect. With respect to the other three V-Dem control variables, we will prepare four configurations for each model: one for each of the three variables being included individually, and another that includes all three in the same model.

We therefore plan to test the following models, in the notation of the R 'lme4' package:

Muthukrishna index

Core trait list @Subchapter level

```
1.  lmer(h2 ~ var_muth + (1|h2_type) + (1|traitsA_subch) + (1|country))
2.  lmer(h2 ~ var_muth + e_migdppc + (1|h2_type) + (1|traitsA_subch) + (1|country))
3.  lmer(h2 ~ var_muth + e_peaveduc + (1|h2_type) + (1|traitsA_subch) + (1|country))
4.  lmer(h2 ~ var_muth + e_wb_pop + (1|h2_type) + (1|traitsA_subch) + (1|country))
5.  lmer(h2 ~ var_muth + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) +
    (1|traitsA_subch) + (1|country))
```

Core trait list @Domain level

```
6.  lmer(h2 ~ var_muth + (1|h2_type) + (1|traitsA_dom) + (1|country))
7.  lmer(h2 ~ var_muth + e_migdppc + (1|h2_type) + (1|traitsA_dom) + (1|country))
8.  lmer(h2 ~ var_muth + e_peaveduc + (1|h2_type) + (1|traitsA_dom) + (1|country))
9.  lmer(h2 ~ var_muth + e_wb_pop + (1|h2_type) + (1|traitsA_dom) + (1|country))
10. lmer(h2 ~ var_muth + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) + (1|traitsA_dom)
    + (1|country))
```

Expanded trait list @Subchapter level

```
11. lmer(h2 ~ var_muth + (1|h2_type) + (1|traitsB_subch) + (1|country))
12. lmer(h2 ~ var_muth + e_migdppc + (1|h2_type) + (1|traitsB_subch) + (1|country))
13. lmer(h2 ~ var_muth + e_peaveduc + (1|h2_type) + (1|traitsB_subch) + (1|country))
14. lmer(h2 ~ var_muth + e_wb_pop + (1|h2_type) + (1|traitsB_subch) + (1|country))
15. lmer(h2 ~ var_muth + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) +
    (1|traitsB_subch) + (1|country))
```

Expanded trait list @Domain level

```
16. lmer(h2 ~ var_muth + (1|h2_type) + (1|traitsB_dom) + (1|country))
17. lmer(h2 ~ var_muth + e_migdppc + (1|h2_type) + (1|traitsB_dom) + (1|country))
18. lmer(h2 ~ var_muth + e_peaveduc + (1|h2_type) + (1|traitsB_dom) + (1|country))
19. lmer(h2 ~ var_muth + e_wb_pop + (1|h2_type) + (1|traitsB_dom) + (1|country))
20. lmer(h2 ~ var_muth + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) + (1|traitsB_dom)
    + (1|country))
```

Uz domain-general index

Core trait list @Subchapter level

```
21. lmer(h2 ~ var_uzDG + (1|h2_type) + (1|traitsA_subch) + (1|country))
22. lmer(h2 ~ var_uzDG + e_migdppc + (1|h2_type) + (1|traitsA_subch) + (1|country))
23. lmer(h2 ~ var_uzDG + e_peaveduc + (1|h2_type) + (1|traitsA_subch) + (1|country))
24. lmer(h2 ~ var_uzDG + e_wb_pop + (1|h2_type) + (1|traitsA_subch) + (1|country))
25. lmer(h2 ~ var_uzDG + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) +
    (1|traitsA_subch) + (1|country))
```

Core trait list @Domain level

```
26. lmer(h2 ~ var_uzDG + (1|h2_type) + (1|traitsA_dom) + (1|country))
27. lmer(h2 ~ var_uzDG + e_migdppc + (1|h2_type) + (1|traitsA_dom) + (1|country))
28. lmer(h2 ~ var_uzDG + e_peaveduc + (1|h2_type) + (1|traitsA_dom) + (1|country))
29. lmer(h2 ~ var_uzDG + e_wb_pop + (1|h2_type) + (1|traitsA_dom) + (1|country))
30. lmer(h2 ~ var_uzDG + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) + (1|traitsA_dom)
    + (1|country))
```

Expanded trait list @Subchapter level

```
31. lmer(h2 ~ var_uzDG + (1|h2_type) + (1|traitsB_subch) + (1|country))
32. lmer(h2 ~ var_uzDG + e_migdppc + (1|h2_type) + (1|traitsB_subch) + (1|country))
33. lmer(h2 ~ var_uzDG + e_peaveduc + (1|h2_type) + (1|traitsB_subch) + (1|country))
34. lmer(h2 ~ var_uzDG + e_wb_pop + (1|h2_type) + (1|traitsB_subch) + (1|country))
35. lmer(h2 ~ var_uzDG + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) +
    (1|traitsB_subch) + (1|country))
```

Expanded trait list @Domain level

```
36. lmer(h2 ~ var_uzDG + (1|h2_type) + (1|traitsB_dom) + (1|country))
37. lmer(h2 ~ var_uzDG + e_migdppc + (1|h2_type) + (1|traitsB_dom) + (1|country))
38. lmer(h2 ~ var_uzDG + e_peaveduc + (1|h2_type) + (1|traitsB_dom) + (1|country))
39. lmer(h2 ~ var_uzDG + e_wb_pop + (1|h2_type) + (1|traitsB_dom) + (1|country))
40. lmer(h2 ~ var_uzDG + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) + (1|traitsB_dom)
    + (1|country))
```

Uz domain-specific index

Core trait list @Subchapter level

```
41. lmer(h2 ~ var_uzDS + (1|h2_type) + (1|traitsA_subch) + (1|country))
42. lmer(h2 ~ var_uzDS + e_migdppc + (1|h2_type) + (1|traitsA_subch) + (1|country))
43. lmer(h2 ~ var_uzDS + e_peaveduc + (1|h2_type) + (1|traitsA_subch) + (1|country))
44. lmer(h2 ~ var_uzDS + e_wb_pop + (1|h2_type) + (1|traitsA_subch) + (1|country))
45. lmer(h2 ~ var_uzDS + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) +
    (1|traitsA_subch) + (1|country))
```

Core trait list @Domain level

```
46. lmer(h2 ~ var_uzDS + (1|h2_type) + (1|traitsA_dom) + (1|country))
47. lmer(h2 ~ var_uzDS + e_migdppc + (1|h2_type) + (1|traitsA_dom) + (1|country))
48. lmer(h2 ~ var_uzDS + e_peaveduc + (1|h2_type) + (1|traitsA_dom) + (1|country))
49. lmer(h2 ~ var_uzDS + e_wb_pop + (1|h2_type) + (1|traitsA_dom) + (1|country))
50. lmer(h2 ~ var_uzDS + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) + (1|traitsA_dom)
    + (1|country))
```

Expanded trait list @Subchapter level

```
51. lmer(h2 ~ var_uzDS + (1|h2_type) + (1|traitsB_subch) + (1|country))
```

```
52. lmer(h2 ~ var_uzDS + e_migdppc + (1|h2_type) + (1|traitsB_subch) + (1|country))
53. lmer(h2 ~ var_uzDS + e_peaveduc + (1|h2_type) + (1|traitsB_subch) + (1|country))
54. lmer(h2 ~ var_uzDS + e_wb_pop + (1|h2_type) + (1|traitsB_subch) + (1|country))
55. lmer(h2 ~ var_uzDS + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) +
    (1|traitsB_subch) + (1|country))
```

Expanded trait list @Domain level

```
56. lmer(h2 ~ var_uzDS + (1|h2_type) + (1|traitsB_dom) + (1|country))
57. lmer(h2 ~ var_uzDS + e_migdppc + (1|h2_type) + (1|traitsB_dom) + (1|country))
58. lmer(h2 ~ var_uzDS + e_peaveduc + (1|h2_type) + (1|traitsB_dom) + (1|country))
59. lmer(h2 ~ var_uzDS + e_wb_pop + (1|h2_type) + (1|traitsB_dom) + (1|country))
60. lmer(h2 ~ var_uzDS + e_migdppc + e_peaveduc + e_wb_pop + (1|h2_type) + (1|traitsB_dom)
    + (1|country))
```

Additional model configurations

We will also run each of these models according to the two specifications for the Country variable noted above: One that excludes countries with missing cultural variance data, and another that estimates their cultural variance by averaging across neighboring countries. We expect all these models to show robustness in revealing the same basic insight – a negative relationship between cultural variance and heritability, at least for the culturally transmissible traits.

6) Describe exactly how outliers will be defined and handled, and your precise rule(s) for excluding observations.

There will be no exclusion-criteria for outliers among observations, but we will exclude observations in the MaTCH database for which no heritability estimate is provided across any of the four heritability study types (for many traits in the dataset, outcome measures other than heritability are reported). For each model, we will exclude all observations in which data for any of the variables included in the model is missing.

Furthermore, we will only analyze traits that we consider to be culturally transmissible. We construct two lists of traits for this purpose, one that excludes traits in the Psychiatric domain, and another that includes them. The first nonpsychiatric list includes the following 19 Subchapter-level traits across 5 Domains (indicated in square brackets):

Core list of traits

- [Activities]: 'Looking after One's Health'
- [Cognitive]: 'Attention Functions', 'Calculation Functions', 'Global Psychosocial Functions', 'Higher-Level Cognitive Functions', 'Intellectual Functions', 'Memory Functions', 'Mild Mental Retardation', 'Psychomotor Functions'

• [Environment]: 'Basic Interpersonal Interactions', 'Informal Social Relationships', 'Education', 'Potential Health Hazards Related to Socioeconomic and Psychosocial Circumstances', 'Problems Related to Upbringing'

• [Social Interactions]: 'Complex Interpersonal Interactions'

• [Social Values]: 'Individual Attitudes of Strangers', 'Societal Attitudes', 'Religion and Spirituality'

Expanded list of traits

For the psychiatric-included list, we add to the above another set of traits in the Psychiatric domain that also fall under 'Mental and Behavioural Disorders' at the Chapter level. We exclude the trait 'Sleep functions' as we consider it as being in a separate category from strictly psychiatric traits. The final list of psychiatric traits is as follows:

• [Psychiatric]: 'Bipolar Affective Disorder', 'Conduct Disorders', 'Dementia In Alzheimer Disease', 'Depressive Episode', 'Disorders of Social Functioning with Onset Specific to Childhood and Adolescence', 'Dissocial Personality Disorder', 'Eating Disorders', 'Emotional Disorders with Onset Specific to Childhood', 'Emotionally Unstable Personality Disorder', 'Habit and Impulse Disorders', 'Hyperkinetic Disorders', 'Mental and Behavioural Disorders Due to Multiple Drug Use and Use of Other Psychoactive Substances', 'Mental and Behavioural Disorders Due to Use of Alcohol', 'Mental and Behavioural Disorders Due to Use of Cannabinoids', 'Mental and Behavioural Disorders Due to Use of Cocaine', 'Mental and Behavioural Disorders Due to Use of Hallucinogens', 'Mental and Behavioural Disorders Due to Use of Opioids', 'Mental and Behavioural Disorders Due to Use of Sedatives or Hypnotics', 'Mental and Behavioural Disorders Due to Use of Tobacco', 'Mood [Affective] Disorders', 'Obsessive-Compulsive Disorder', 'Other Anxiety Disorders', 'Pervasive Developmental Disorders', 'Phobic Anxiety Disorders', 'Reaction to Severe Stress, and Adjustment Disorders', 'Recurrent Depressive Disorder', 'Schizophrenia', 'Schizotypal Disorder', 'Specific Personality Disorders', 'Temperament and Personality Functions'

7) How many observations will be collected or what will determine sample size?
No need to justify decision, but be precise about exactly how the number will be determined.

We are using all data available, so sample size is strictly determined by the specifications detailed above. We expect to be under-powered.

8) Anything else you would like to pre-register?
(e.g., secondary analyses, variables collected for exploratory purposes, unusual analyses planned?)

Before writing this preregistration, we had performed an exploratory analysis of some of the data. In particular we had run Pearson's correlation analyses and created scatter plots for a number of trait-groups from the MaTCH dataset (Polderman et al., 2015) against Uz's (2015) Domain-Specific and Domain-General Tightness-Looseness measures. The trait-groups that we looked at were the following:

- All available traits within the ICF/ICD10 chapter ‘Cognitive’
- All available traits within the ICF/ICD10 subchapter ‘Conduct Disorders’
- All available traits within the ICF/ICD10 subchapter ‘Depressive Episode’
- All available traits within the ICF/ICD10 subchapter ‘Higher-level Cognitive Functions’
- All available traits within the ICF/ICD10 chapter ‘Mental and Behavioural Disorders’
- All available traits within the ICF/ICD10 chapter ‘Mental Functions’
- All available traits within the ICF/ICD10 subchapter ‘Temperament and Personality Functions’

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Changes to pre-registration for 'cultural variance and heritability'

Our original analysis plan was pre-registered on the Open Science Framework on 24 Oct 2019 (with 1 year embargo).

Description of change

In order to mitigate the impact that cross-control variation in answering style may have on the results of their analysis, Muthukrishna et al. (under review) often collapsed graded responses to WVS questions into 2 (positive or negative) or 3 (positive, neutral, or negative) discrete "alleles". The downside of this procedure is that it reduces the amount of potentially meaningful variation. Because the heritability data for the traits that we consider to be culturally malleable are both few in number and also concentrated in WEIRD countries that are relatively similar to each other (e.g., US, UK, Australia), we will create and test a version of the Muthukrishna index of cultural variation that does not collapse graded responses.

In particular, we will use the raw WVS data of same questions and the same years as those used in Muthukrishna et al. (under review). After dropping all data points that contain a missing or invalid value (i.e., all responses coded as a negative number in the WVS codebook), we will rescale all of the non-nominal variables using min-max normalization, which is given by the following formula:

$$x' = \frac{x - \min(x)}{\max(x) - \min(x)}$$

where *x* is an original value and *x′* is a normalized value. We will then compute the variance for all of the rescaled variables, thereby obtaining the cultural variance for the uncollapsed variables and yielding a modified version of the Muthukrishna index.

Additional information to report

Prior to the implementation of the above change, we had already run analyses according to the method detailed in our initial pre-registration. The results of analyses were ambiguous, and the effect of the Muthukrishna index was considerably weaker than the Uz (2014) index, despite the two indices being constructed from different waves of the same global survey. One important difference between the two indices is that the Muthukrishna index collapses graded responses while the Uz index does not. We expect that the above change in the method by which we construct the variable will increase its effect on heritability and give a clearer signal of the relationship that we predict in the initial pre-registration.

A further specification

In our previous pre-registration, we did not specify exactly which countries we would use to infer the cultural variance of the missing ones (for which we also have heritability data). For Belgium, we will take the average of France, Netherlands, and Germany. For Denmark, we will take the average of Germany and Sweden. We have not yet examined how the ascription of these data affect the result of the analyses.

References

Muthukrishna, M., Bell, A. V., Henrich, J. and Curtin, C. M., Gedranovich, A., McInerney, J., & Thue, B (under review). Beyond WEIRD psychology: Measuring and mapping scales of cultural and psychological distance. http://dx.doi.org/10.2139/ssrn.3259613

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Chapter 5: Cross-cultural variation in the structure of internal representations

Introduction

Much of what we commonly think of as cultural differences consist of differences in behavior. Cross-cultural differences in communication, cooperation, rituals, mating, eating, work, and leisure are apparent across the globe. Even when we talk about differences of mentality or attitude between cultural groups, we typically infer such psychological attributes through the lens of observable behavioral differences. But there are also many aspects of our psychology that are not expressed as overt behavior, and that remain opaque to casual observation and even to controlled experimental study. Inferring the internal cognitive machinery that underpins behavior is an inverse problem that is intimately linked to the problem of how to think about internal representations, here defined as the informational structures of the mind that model and track the structure of the world (S. Edelman, 2008). In order to understand cultural variation at the level of mental processes themselves, we must understand variation in internal representations.

For a long time, many researchers believed that variation in internal representations was not a problem to be considered. During the advent of cognitive science, the ascendant view held that minds modeled the world around them by employing logical operations over abstract internal symbols (Neisser, 1967; Newell, 1980; Simon & Newell, 1971). On this view, any apparent variation in mental organization—whether between individuals or cultures—was only in surface appearance, and the underlying machinery was invariant along the dimensions that scientifically mattered. This strict computationalist view of the mind has since been tempered due to advances in several areas. On the one hand, a deeper understanding of the nervous system revealed it unlikely to be organized like a digital computer; on the other hand, researchers working in areas like vision and psycholinguistics succeeded in both engineering and reverse-engineering a class of biologically plausible systems that perform psychological operations without symbol manipulation (e.g., Braitenberg, 1984; Brooks, 1991; Elman et al., 1996; Gibson, 1979; Rumelhart et al., 1986). Although there remain aspects of human cognition that might only be sufficiently explained by an updated symbolic framework (Frankland & Greene, 2020; Penn et al., 2008; Piantadosi et al., 2016; Sablé-Meyer et al., 2021), this theoretical shift has revealed how the mind is populated by internal representations that are better approximated as re-instantiations of perceptual and motor processes than as amodal symbols that generate meaning by being passed through logical operations (Barsalou, 1999, 2008; Gallese & Lakoff, 2005; Kiefer & Pulvermüller, 2012; Kosslyn et al., 2001). This sensorimotor or "analog" view of internal representation conforms better to what is known about the architecture of the brain (e.g., its topographic organization and hierarchical processing) than a symbolic account does. It also accords better with our subjective experience of mental phenomena such as visual imagery and episodic memory without requiring contorted explanations for their subjective phenomenology.

Research over the past few decades has revealed much about the psychological and neurofunctional organization of these sensorimotor representations at an aggregate level, but relatively little is known about their variation. One area in which researchers have made headway is in the study of individual variation in the qualitative structure of sensorimotor representations, sometimes referred to as *cognitive style*[20] (Kozhevnikov, 2007; Witkin & Moore, 1977). Cognitive style reflects consistent differences in people's mode or strategy of information processing, typically taking the form of a trade-off between strategies rather than being an aptitude measure. Although this kind of individual-level variation is frequently treated as noise in the design of cognitive experiments, a fine-grained analysis can offer a deeper understanding of underlying cognitive mechanisms (see Ansari et al., 2003; Karmiloff-Smith et al., 2004; Kosslyn et al., 2002; Noppeney, Penny, et al., 2006; Noppeney, Price, et al., 2006). A standard example of cognitive style is the visualizer–verbalizer continuum, (Kirby et al., 1988; Mayer & Massa, 2003; for neuroscience evidence see Kraemer et al., 2009; Kraemer et al., 2014), which can be further decomposed for example into visualizers who excel at processing objects, more common among artists, and visualizers who excel at processing spatial structures,

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[20] There are other similar constructs such as "learning style" (A. Y. Kolb & Kolb, 2005) and "thinking style" (Sternberg & Grigorenko, 1997), which have been studied intensively in applied fields such as education and management. However, these lines of research have led to a proliferation of proposed styles (Kozhevnikov et al., 2014; Riding & Cheema, 1991), and their emphasis on complex outcomes such as school or workplace performance tends to lead us away from our present focus on the basic organization of internal representations.

more common among scientists and engineers (Blazhenkova & Kozhevnikov, 2010; Kozhevnikov et al., 2005).

In parallel with the study of individual differences in cognitive style within populations, there has also been a substantial body of work on cultural variation in cognitive style. This research is nested within a larger body of work on cross-cultural differences in perception and cognition writ large, which has uncovered significant variation in domains ranging from memory (Wang, 2021) and spatial cognition (Majid et al., 2004) to moral judgments (Barrett et al., 2016) and economic decision-making (Henrich et al., 2005; House et al., 2020). Cross-cultural psychological variation had been insufficiently explored for decades due to the WEIRD (Western, educated, industrialized, rich, democratic) people problem in the psychological and behavioral sciences (Apicella et al., 2020; Barrett, 2020; Henrich et al., 2010). A foundational discovery within this field was the finding that Western people tend to adopt an "analytic" cognitive style, which includes features such as attention to focal objects, ascription of causality to agents, and use of abstract categories, whereas East Asians tend to adopt a "holistic" cognitive style, with features such as attention to relationships among elements in the perceptual field, ascription of causality to situations, and use of relational categories (I. Choi et al., 1999; Kitayama et al., 2003b; Masuda & Nisbett, 2001).

The divergence in cognitive styles occurs not only between East and West, but also among Eastern countries and among Western countries (Kitayama et al., 2009), as well as among regions within countries (Kitayama et al., 2006; Talhelm et al., 2014). These studies have linked the divergence in cognitive styles to historical factors such as subsistence method or frontier activity, each of which have ramifications for demands on social structure (e.g., degree of interdependence), and which may be linked to socio-psychological variables such as the strength of social norms (Talhelm & English, 2020) or the perceived relationship between self and society (Markus & Kitayama, 1991). Recent evidence suggests that the underlying explanatory variable may instead be kinship intensity (J. F. Schulz et al., 2019). The causal processes linking these societal factors to cognition and perception—how we think about and see the world—are not well understood (for a possible explanatory contribution, see Kitayama et al., 2009). At a proximal level, there is evidence of caretaker-to-child transmission of culturally typical cognitive styles via joint attention and shared discourse (Senzaki et al., 2016;

see also Wang, 2001), but the missing piece in this overall picture is the population-level dynamics that induces systematic divergence across cultures.

Much of the work on cultural differences in internal representation has relied on the contrast between analytic and holistic processing. Analytic–holistic cognitive style has been repeatedly deployed as an explanation in the context of cultural variation, but it does not appear to be able to explain variation among individuals within a culture (Kitayama et al., 2009; Na et al., 2010). Analytic–holistic cognitive style is thus likely to be a group-level trait that is generated by forces acting upon the cultural group itself as a unit. However, these results conflict with the sizeable literature on individual differences in cognitive style mentioned above (Kozhevnikov, 2007; Witkin & Moore, 1977). This literature does find substantial variation within samples of individuals with the same cultural background, often for dimensions of variation that are highly similar to analytic–holistic processing (e.g., Allinson & Hayes, 1996). This discrepancy motivates a reassessment of cognitive style and indeed the structure of internal representations in general. There may be dimensions of variation that better capture the variation in the structure of internal representations than analytic–holistic processing, while remaining consistent with established findings.

In the present study, I use the Internal Representations Questionnaire (IRQ; Roebuck & Lupyan, 2020) to investigate cross-cultural differences in the structure of internal representations. The IRQ is an instrument designed to probe individual differences in modalities of thought. In the original study, conducted with a US sample, a factor analysis reveals a 4-modality structure: visual imagery, internal verbalization, orthographic imagery, and representational manipulation. The last refers to the ability to dynamically manipulate mental representations regardless of modality, as captured by items such as “I can easily imagine the sound of a trumpet getting louder”. Visual imagery and internal verbalization have been widely studied, but orthographic imagery and representational manipulation constitute novel modalities that are not typically discussed in the literature. Importantly, responses to the IRQ also predict performance on a cue-target matching task in a modality-selective manner, confirming predictive validity with respect to behavioral consequences.

Although the IRQ reveals notable findings about the population structure of internal representations, it is not immediately clear how much of this structure can be attributed to the effect of genes, culture, or individual experience. Without such an understanding, we do not know the degree of plasticity or adaptability of mental representations, nor the extent to which they are amenable to interventions in contexts such as education, professional training, or psychotherapy. A cross-cultural analysis is an important step toward obtaining insight about the generative processes that create these cognitive phenotypes. In particular, I collect data from Japan and China, two populations that differ from the original US sample across several social and cultural dimensions that may be relevant to the structure of mental representations. My focus here will be on their different writing systems. Whereas English is written in a phonetic alphabet, Chinese writing is logographic and thus locates a semantic meaning in each character (as well as a sound). Japanese writing makes heavy use of Chinese-derived logograms, but whereas Chinese logograms are organized in a one-to-one mapping between character and sound, Japanese logograms are commonly associated with multiple sounds. Moreover, the Japanese writing complements its logographic system with two additional phonetic syllabaries, yielding a hybrid script that shares features of both the English and Chinese systems.

I test the hypothesis that differences in writing systems explain differences in the structure of mental representations. The IRQ identifies orthographic imagery as a coherent modality of thought, so the development of this faculty may be plausibly impacted by the properties of the particular orthographic input. Neuroimaging studies find differences in the profile of neural activation between Chinese and English reading (Perfetti et al., 2013; Wu et al., 2012), and there are several behavioral and cognitive differences that emerge during acquisition of these writing systems as well (McBride, 2016). Because reading reorganizes the brain not only in areas that directly subserve reading but also in areas devoted to other functions through downstream effects (for example face perception; Dehaene et al., 2015), the effect of exposure to a given writing system may extend beyond orthographic imagery into other modalities of internal representation as well. Due to its relative recency in human history, literacy is generally acknowledged to be a cultural adaptation rather than a genetic one. Therefore, an understanding of how writing systems shape internal representations can help us understand more generally how culture shapes the human mind.

Methods

Preregistration

I preregistered a number of details about the study and its analysis following the format of AsPredicted [https://aspredicted.org]. Preregistrations were submitted twice—once during collection of the Japanese data (but before anyone was able to see the data), and once more prior to collection of the Chinese data. Both submissions are made public at the Open Science Framework at the URL [https://osf.io/nxmg2/], and also included in the Appendix of this chapter.

The Japanese preregistration specified details such as exclusion criteria for participants, expected sample size, the procedure of questionnaire administration, and the translations of the items. With respect to the analysis, I simply stated that I would follow the same analysis as performed in Roebuck and Lupyan (2020). Only after the Japanese data were collected and analysed was additional collection of Chinese data decided. The Chinese preregistration was thus written with the findings from the Japanese data in mind, such as differences in mean scores across the original 4 IRQ factors between the US and Japanese samples. In the Chinese preregistration, I included several predictions for how demographic variables would be associated with factor scores in the Chinese data. More detail overall was included in the Chinese preregistration, such as the method for standardizing the data (i.e., within-culture standardization) and rough specifications for statistical tests.

In both the Japanese and Chinese preregistrations, I indicated expected sample sizes but also noted that the final sample size would depend upon the depletion of funds. The exact sample size obtainable with the available budget was uncertain due to the fee systems adopted by the survey management companies. The Japanese sample size turned out to be slightly larger than the initial expected number, and the Chinese sample size turned out to be slightly smaller. In the Chinese preregistration, the exclusion criteria were made slightly more stringent than in the Japanese preregistration, due to patterns of responses found in some participants in the Japanese data. In the final analysis of the Japanese data described below, I retroactively applied the more stringent exclusion criteria from the Chinese preregistration for consistency. There was no meaningful difference in the outcomes that depended on which set of criteria was adopted.

One major difference between the preregistered analysis plan and the final analysis below is the addition of a confirmatory factor analysis for both the Japanese and Chinese data, and an exploratory factor analysis for the Chinese data. These analyses were planned post hoc, only after all of the data were collected and examined. Because the confirmatory factor analysis suggested that the factor structure extracted by Roebuck and Lupyan (2020) for their US sample was compatible with neither the Japanese nor Chinese data, I omitted a mixed effects model analysis that I had declared in the Chinese preregistration. This analysis would have compared item responses to mean scores on the US factor structure across the three societies. Including this model would have reified the US factor structure despite it likely being an unfit metric to describe the structure of the Chinese and Japanese data. Moreover, the mixed effects model did not yield any meaningful information beyond what is captured in the t-tests shown in abbreviated form (i.e., with significance only) in **fig. 2**. Similarly, although I had made predictions about how demographic variables of the Chinese participants would be associated with scores for the US factors, I omitted this analysis because the confirmatory factor analysis suggested that these factors were likely to be an unfit metric for the Chinese data. Instead I performed the same analysis using the factor structure that was extracted from the Chinese data with exploratory factor analysis.

Participants

I recruited participants in China and Japan through survey management companies in each of the two countries. The Chinese company was approached with the help of a Chinese collaborator. The Japanese sample consisted of 122 individuals who offered consent for participation, but 22 (18%) met the exclusion criteria by either failing one of the two attention check questions or by giving the same Likert response to 90% or more of the main questionnaire items. When preregistering exclusion criteria for the Japanese sample, I had originally proposed to exclude participants who gave the same response on *all* items, but because there turned out to be a small number of participants in this sample who gave the same response on not strictly all but almost all items, I subsequently broadened the criterion to 90%

when preregistering for the subsequent Chinese sample. For consistency, I then retroactively applied this broader criterion to the Japanese sample, but this did not impact the results in any meaningful way. The Chinese sample consisted of 470 individuals who offered consent. There was just 1 participant who failed any of the exclusion criteria, suggesting that the Chinese data might be of significantly better quality than the Japanese data. There were 2 participants who were excluded due to uninterpretable results likely arising from a bug, and the final Chinese sample size was 467.

For the Japanese sample, the gender makeup was 57 (57%) males and 43 (43%) females, and the mean age was 53.7 with a range of 21 to 72, with 81% of the sample aged 45 or above (**Figure 5.1a**). For the Chinese sample, the gender makeup was 234 (50%) males and 233 (50%) females, and the mean age was 31.5 years, resulting in a considerably younger group than the Japanese sample: the age range was 20 to 70 but 87% of the sample were in their 20s or 30s (**Figure 5.1b**). For the Chinese sample, we also obtained responses for several demographic and background variables beyond age and gender: years of education, hours per week spent on dense reading (e.g., books and newspapers but not social media), frequency of thinking in English, and frequency of using English in daily life (**Figure 5.1c–f**).

The researchers paid the survey management companies, and participants were compensated by these companies for undisclosed amounts of payment. The research funds were provided by the London School of Economics Department of Psychological Science, and the number of participants to be included in the study was determined by the available budget. Ethical approval for the study was granted by the London School of Economics Research and Innovation Division and the Department of Psychological and Behavioural Science (case #19583).

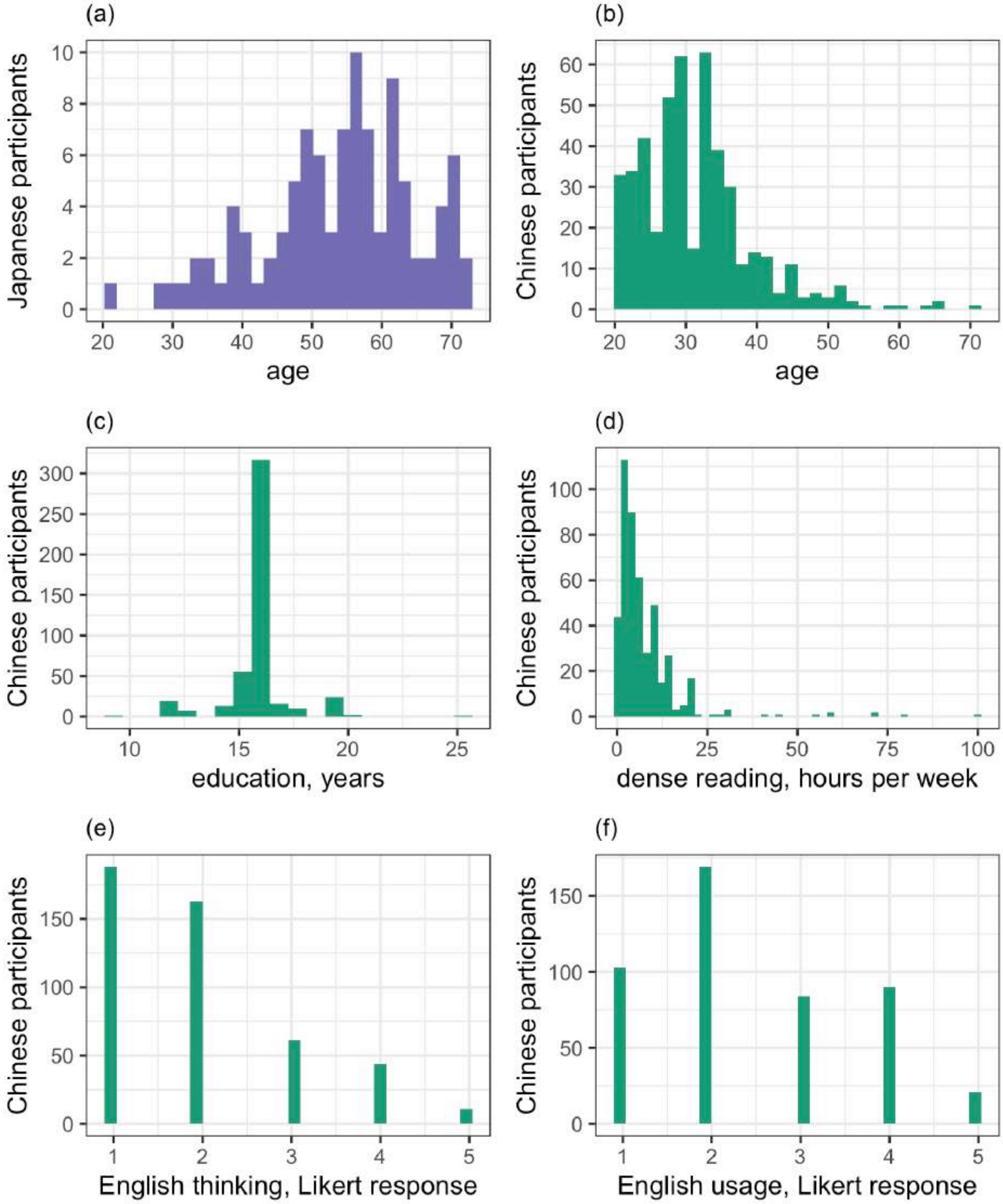

Figure 5.1: Self-reported demographic characteristics of the Japanese (a) and Chinese (b–f) samples.

Instrument

I administered the Internal Representations Questionnaire (IRQ; Roebuck & Lupyan, 2020) after it was translated into Chinese by a collaborator and into Japanese by myself, both translators being fully literate in their respective languages. The IRQ consists of 36 items that probe the use of different forms of mental representation in everyday life. The questionnaire was originally constructed with the motivation of investigating internal verbalization and its effect in shaping perceptual and cognitive processing, but the authors ultimately found 4 factors that each represent a different modality of internal representation: visual imagery, internal verbalization, orthographic imagery, and representational manipulation. The items in the IRQ were selected through an exploratory factor analysis on US samples consisting of university students and workers on Amazon Mechanical Turk. The items of the IRQ and their factor assignment in the original study are listed in **Table 5.9**.

For both groups, the IRQ was administered through a smartphone interface built by the survey management companies. For each item, participants were required to select a response from a 5-point Likert scale that consisted of the options "strongly disagree", "disagree", "neither agree nor disagree", "agree", and "strongly agree". There were two reverse-coded items (items 13 and 33) whose responses were inverted during data analysis to have the same directionality as the other items. The main questionnaire items were preceded by a consent question that allowed participants to opt-out of the study. The order of presentation of the main items was randomised, and the participant could only complete the study by providing responses for all questions. Two attention check questions were presented at randomized positions in between the main items.

Overview of analysis

I first conducted simple comparisons of observed scores across the IRQ factors. The Chinese and Japanese scores were compared to the scores of the US sample in Roebuck and Lupyan (2020; data published in online repository: https://osf.io/8rdzh/). Comparisons were made using both raw scores and within-culture standardized scores, the latter being a strategy to control for cross-cultural differences in response style (Fischer, 2004). As this comparison of observed scores was conducted without verification of the IRQ factor structure in the Chinese and Japanese samples, I performed a confirmatory factor analysis to evaluate the fit of the IRQ factors to the non-US samples and to test measurement invariance. The results were mixed, but taken in total suggested inadequate fit. To identify the difference in factor structure between the US and non-US data, I conducted an exploratory factor analysis but only for the Chinese data, as the sample size of the Japanese data was insufficient. Finally, I obtained factor scores for the newly extracted factors across the Chinese participants, and entered them into a regression analysis with the demographic variables entered as predictors and the factor scores as outcomes.

Results

Cross-cultural comparison of observed scores

Comparison of raw scores

A comparison of raw observed scores between the 3 samples revealed salient cultural differences (**Table 5.1** and **Figure 5.2**, top panel). The mean scores across all responses for the US, Chinese, and Japanese samples were 3.51, 3.52, and 3.15, respectively. Therefore, the magnitude of US and Chinese responses were roughly similar on average, and both were about one-third of a Likert point higher than the Japanese responses. Despite their overall similarity in magnitude, US responses were considerably (more than half a Likert point) lower than Chinese responses on items associated with orthographic imagery. US responses were slightly higher than Chinese responses on items associated with the visual imagery and internal verbalization factors.

Japanese responses on average were lower than both the US and Chinese responses for visual imagery, internal verbalization, and representational manipulation. As the Japanese scores were closer to the mid-point of the 5-point Likert scale, this pattern may reflect either a middle response bias as previously reported in this population (Chen et al., 1995; Tasaki & Shin, 2017), or a negative response bias relative to the US and Chinese samples. Despite their overall lower scores, Japanese participants were at roughly the same level as the US participants for items that load onto the orthographic imagery factor, although still lower than Chinese participants.

Comparison of standardized scores

Within-culture standardized responses revealed cultural differences that are more readily interpretable than the raw score comparisons (**Table 5.1** and **Figure 5.2**, bottom panel). Within each population, the mean score was set to 0 and a standard deviation in the data was scaled to 1 for this analysis. All 3 groups yielded the highest scores on items that load onto the visual imagery factor, followed by items that load onto the internal verbalization factor. Scores for both of these factors were higher than scores for representational manipulation across all 3 groups.

The greatest cross-cultural variation was observed in the orthographic imagery factor: US scores for these items were about half a standard score lower than the Chinese scores and about a third of a standard score lower than the Japanese scores (US, $z = -0.66$; China: $z = -0.17$; Japan, $z = -0.32$). Orthographic imagery scores were thus particularly high in the two Asian samples compared to the US, and Chinese scores were slightly higher than Japanese scores. The US sample had noticeably higher scores on items that load onto the internal verbalization factor compared to the Japanese and Chinese samples. There are several other differences that can be statistically detected, but the findings above are relatively pronounced patterns that can be readily discerned from the standardized data. Taken at face value, these results suggest that orthographic imagery occupies a more prominent role in the inner mental life of Chinese and Japanese participants more than it does for participants in the US. The results also suggest that participants in the US may make greater use of internal verbalization than Chinese and Japanese participants.

There is no clear answer to what standardization procedure is most adequate in an analysis like this one, and the within-culture standardization approach that I adopt here is among the common methods employed in analysis of cross-cultural questionnaires (Fischer, 2004). I also tried an alternative method in which scores are standardized within individuals, yielding what are known as ipsative scores (Baron, 1996), but the change in mean scores for the factors was on the order of 0.002 to 0.02 standard scores, negligible for practical purposes.

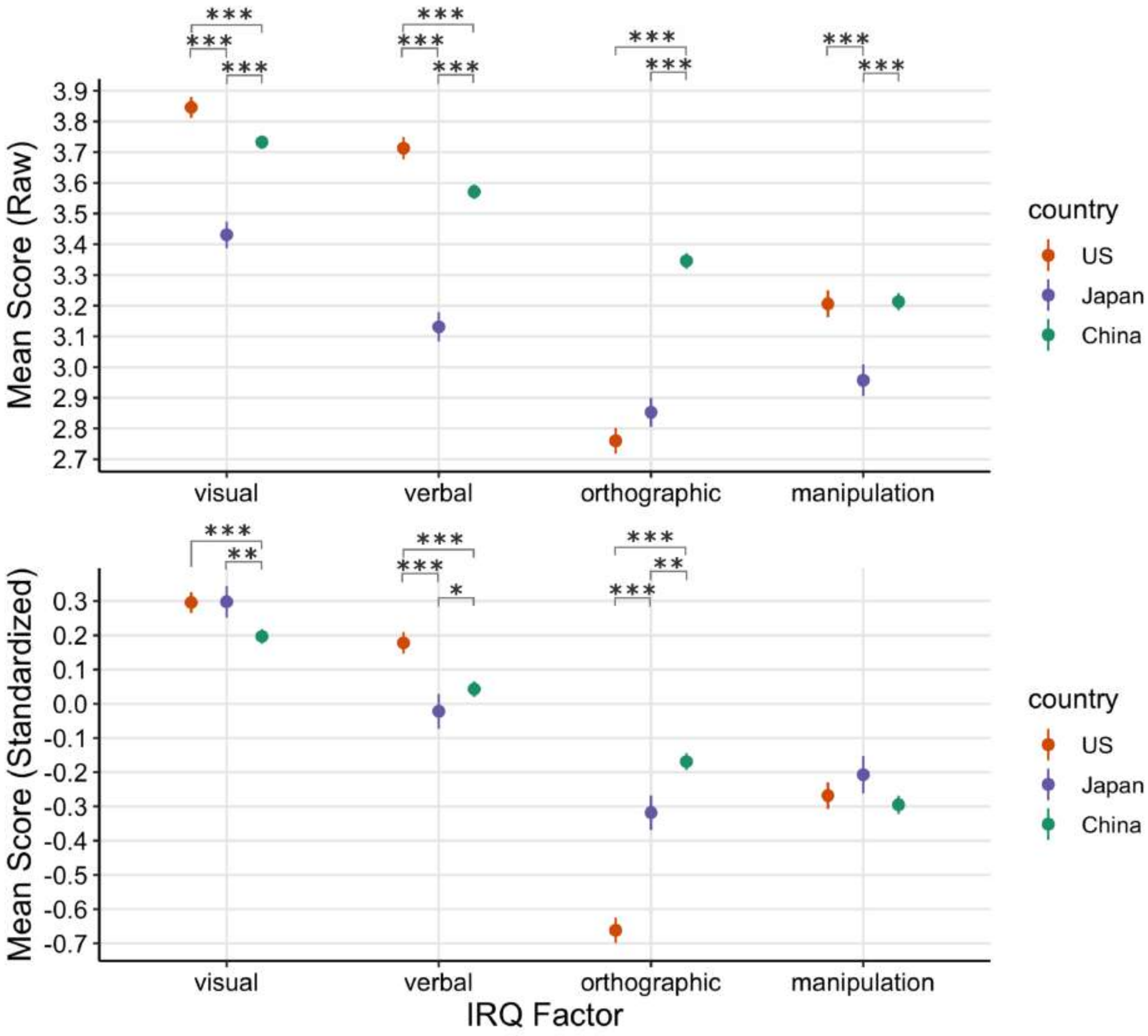

Figure 5.2: Comparison of raw means and within-culture standardized means of item responses grouped according to the factor structure extracted in Roebuck & Lupyan (2020). The US values are computed from data published by Roebuck & Lupyan (2020). Error bars are standard errors, and statistical significance levels derived from pairwise t-tests are indicated by asterisks (*: p<.05; **: p<.01; ***: p<.001).

Table 5.1: Results of t-tests for simple pairwise comparison of mean scores between US, Japanese (JP), and Chinese (CN) samples, for the 4 factors extracted from the US data in Roebuck and Lupyan (2020). The US values are computed from data published by Roebuck & Lupyan (2020).

Raw					Standardized				
Factor	Countries	*t*	*df*	*p*	Factor	Countries	*t*	*df*	*p*
Visual	US–JP	11.44	2181	<.0001	Visual	US–JP	–0.06	1832.1	0.950
	US–CN	4.27	4250	<.0001		US–CN	4.12	4532	<.0001
	JP–CN	–9.32	1573	<.0001		JP–CN	3.00	1445	0.003
Verbal	US–JP	16.52	2609	<.0001	Verbal	US–JP	5.67	2193	<.0001
	US–CN	5.55	5065	<.0001		US–CN	5.81	5400	<.0001
	JP–CN	–14.00	1871	<.0001		JP–CN	–1.99	1722	0.046
Orthographic	US–JP	–1.67	1506	0.095	Orthographic	US–JP	–6.23	1263	<.0001
	US–CN	–13.59	2250	<.0001		US–CN	–12.72	2386	<.0001
	JP–CN	–10.48	947	<.0001		JP–CN	–3.03	870	0.003
Manipulation	US–JP	4.39	1435	<.0001	Manipulation	US–JP	–1.08	1202	0.280
	US–CN	–0.14	2459	0.886		US–CN	0.68	2619	0.494
	JP–CN	–5.18	988	<.0001		JP–CN	1.71	902	0.087

Internal reliability of IRQ factors

To test the internal reliability of the factor structure extracted by Roebuck & Lupyan (2020) in the Chinese and Japanese data, I measured Cronbach's alpha (**Table 5.2**). The alpha coefficients measured in these new data are presented together with the values reported in the original US study for reference (Roebuck & Lupyan, 2020). The reliabilities of the Chinese sample were overall lower than the US values, although mostly falling within a conventionally acceptable range ($\alpha > 0.7$). A noticeably low alpha coefficient was found for the visual imagery factor, whose value of 0.55 was far below that of the same factor in the US study, as well as below the conventional threshold. Reliability in the Japanese sample was at a very similar level to the US sample with the possible exception of the visual imagery factor, which was somewhat lower.

The analysis revealed some items whose removal increased internal reliability. Such increases were largely on the order of $\Delta\alpha = +0.01$, with the exception of one item linked to the visual imagery factor (item 10) in the Chinese sample, whose removal resulted in a large increase of 0.06. This item corresponded to the statement "If I imagine my memories visually they are more often static than moving", suggesting a particularly poor fit of this item with respect to the other visual imagery items for Chinese participants.

Table 5.2: Cronbach's alpha measure of internal consistency for each of the 4 factors extracted from a US sample in the original study. Internal consistency for US data is computed from the raw data published online by Roebuck and Lupyan (2020)[21].

Cronbach's alpha				
	Visual	Verbal	Orthographic	Manipulation
Chinese	0.55	0.74	0.70	0.68
Japanese	0.77	0.85	0.71	0.75
US	0.86	0.86	0.72	0.79

Confirmatory factor analysis

A confirmatory factor analysis of the IRQ factors of Roebuck & Lupyan (2020) with the Chinese and Japanese data offered mixed results. Several goodness-of-fit indices demonstrated inadequate model fit (**Table 5.3**). In the Chinese sample, the criteria recommended by Hu & Bentler (1999), a commonly cited reference, were met for RMSEA and SRMR but not for CFI or for TLI. In the Japanese sample, none of the indices met the recommended criteria. However, this was also the case for the US data set from which the model was initially constructed (Roebuck & Lupyan, 2020)—none of the fit indices successfully met the criteria. Goodness-of-fit measures for the US sample were better than the Japanese sample but worse than the Chinese sample. It was therefore unclear whether the IRQ factor model was a comparatively worse fit for the two new Asian samples compared to the data from the published US sample[22]. Across all 3 samples, CFI and TLI were far from meeting the recommended criteria, while RMSEA and SRMR were fairly close to the threshold even when they fell short, such that under some other more lenient criteria (e.g., Schermelleh-Engel et al., 2003), they would pass as acceptable. A combination of low CFI/TLI and acceptable RMSEA/SRMR likely reflects low correlations among the variables, resulting in a condition

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[21] In Table 5.1 of Roebuck & Lupyan (2020), Cronbach's alpha was 0.79 for the orthographic imagery factor and 0.72 for the representational manipulation factor, while visual imagery and internal verbalization were both 0.86 as computed here. So there is a discrepancy between the published coefficients and the ones computed from the raw data, but I assume this to be a typo rather than a problem with the raw data, and thus enter the computed values in Table 5.1 here.

[22] The US sample tested here is the one that was used to initially construct the IRQ factor model in Roebuck and Lupyan (2020). The authors then followed up this procedure with a confirmatory factor analysis on a separate, larger sample (N=871). They only reported RMSEA for this follow-up analysis and did not publish the raw data, but the reported RMSEA value of 0.52 indicates a better fit than RMSEA for the sample tested here..

where the specified factor model does not sufficiently improve the fit of model to data compared to a null model that includes only variances.

Table 5.3: Goodness-of-fit indices for confirmatory factor analyses with the factor structure extracted by Roebuck & Lupyan (2020). US values are computed from raw data published online by Roebuck & Lupyan (2020).

Goodness-of-fit indices							
Sample	N	χ2	df	RMSEA	SRMR	CFI	TLI
Chinese	467	1187.88	588	0.047	0.061	0.788	0.773
Japanese	100	1022.88	588	0.086	0.1	0.661	0.636
US	222	1201.18	588	0.069	0.098	0.773	0.757

I tested measurement invariance to examine whether combining data from multiple countries worsens the fit of the factor model from the original US study (**Table 5.4**), using the criteria recommended by Rutkowski & Svetina (2014). I conducted this analysis despite the poor fit suggested by some of the fit indices in the confirmatory factor analysis of individual countries described above, so interpretation of the results requires caution.

The aggregated data comprising the US, Chinese, and Japanese samples demonstrated slightly poorer fit than the US data alone, but the difference did not exceed the criteria for configural invariance, thereby suggesting invariance of factor structure between the groups. A test for metric invariance was then conducted by constraining the factor loadings to be equal across the 3 groups. Again, the difference in the fit measures did not exceed the recommended criteria. I followed this with a test for scalar invariance, by constraining the item intercepts to be equal across groups. In this case the change in fit statistics exceeded the criteria due to a large change in CFI, although the change in RMSEA remained small and sub-threshold. The analysis indicated that factor structure (configural invariance) and factor loadings (metric invariance) but not intercepts (scalar invariance) were invariant across the 3 samples under the adopted criteria.

The same series of tests were also conducted in pairwise fashion for the US and Chinese samples and also for the US and Japanese samples. Similarly to the aggregate analysis with all

3 samples, metric but not scalar invariance was established for each of these groupings. The US–Chinese pair demonstrated slightly better fit measures for configural invariance compared to the US-only sample, and the US–Japanese pair demonstrated slightly worse fit. In sum, the fit of the factor loadings extracted in the original study does not noticeably decrease in the Chinese and Japanese samples, although the fit of the item intercepts do, thereby suggesting that the IRQ measures the same constructs across the three sampled cultures, but is limited in the degree to which actual item responses can be directly compared across cultures.

Table 5.4: Tests of measurement invariance for three combinations of samples: {US, China, Japan}, {US, China}, and {US, Japan}, with conventional goodness-of-fit indices.

Measurement Invariance									
Included groups	Invariance test	χ2	df	RMSEA	SRMR	CFI	TLI	ΔCFI	ΔRMSEA
US, China, Japan	Configural	3411.94	1764	0.060	0.074	0.758	0.741		
	Metric	3608.27	1828	0.061	0.082	0.739	0.730	−0.019	0.001
	Scalar	4293.69	1892	0.069	0.090	0.647	0.648	−0.091	0.009
US, China	Configural	2389.05	1176	0.055	0.071	0.781	0.765		
	Metric	2512.24	1208	0.056	0.079	0.764	0.754	−0.016	0.001
	Scalar	2864.00	1240	0.062	0.084	0.706	0.702	−0.058	0.006
US, Japan	Configural	2224.06	1176	0.074	0.096	0.758	0.718		
	Metric	2322.78	1208	0.076	0.097	0.739	0.708	−0.017	0.001
	Scalar	2650.24	1240	0.084	0.107	0.647	0.640	−0.074	0.008

To further assess the adequacy of the original IRQ factor structure for the Chinese and Japanese samples, I inspected the intercorrelations among the factors in the 3 samples. The intercorrelations among the factors were high in the Chinese and Japanese sample, often by a factor of 2 compared to the intercorrelations reported by Roebuck and Lupyan (2020) (**Table 5.5**). This higher degree of similarity among the factors suggests that the IRQ factor structure extracted from the US sample is not appropriately capturing the variance present within the Chinese and Japanese data.

Summarizing this section: I uncovered mixed evidence about the extent to which the IRQ factors fit the Chinese and Japanese data. Several measures showed inadequate fit, but goodness-of-fit was not particularly worse than for the original US sample. Metric invariance was obtained for the three samples in aggregate as well as in a pairwise manner, but scalar invariance was not. The high factor intercorrelations for the Chinese and Japanese sample suggest that the IRQ factors are not nearly as well-separated for the Asian samples as they are in the US sample.

Table 5.5: Intercorrelations among the IRQ factors for the three samples. The US intercorrelations are taken from Ruebuck & Lupyan (2020), Table 5.1.

Factor intercorrelations									
	Chinese			Japanese			US		
IRQ Factor	Visual	Verbal	Ortho.	Visual	Verbal	Ortho.	Visual	Verbal	Ortho.
Visual	~			~			~		
Verbal	0.80	~		0.69	~		0.47	~	
Orthographic	0.70	0.78	~	0.70	0.79	~	0.35	0.38	~
Manipulation	0.60	0.50	0.53	0.82	0.55	0.69	0.42	0.29	0.31

Exploratory factor analysis

Analytical specifications

Due to ambiguous fit of the IRQ factor model with respect to the Chinese and Japanese samples, I conducted an exploratory factor analysis to see whether there is a different factor structure that better captures the pattern of the data from the two East Asian societies. A better model may point us toward meaningful cross-cultural differences in the structure of internal representations.

The Japanese sample (N=100) was considerably smaller than the Chinese sample (N=467). A sample size of 100 falls short of many recommendations for sample size in exploratory factor analysis. The exact recommendation varies and often depends on other aspects of the analysis such as the number of items, the distribution of communalities, and factor loadings. However, judging from various sources (e.g., Fabrigar et al., 1999; Fabrigar & Wegener, 2012; Hair et al., 2009; Matsunaga, 2010), the minimum sample size that is appropriate for the present analysis is around 200 participants. I therefore conducted exploratory factor analysis only for the Chinese sample.

To first select the number of factors to be retained in an exploratory factor analysis of the Chinese data, I employed 3 selection methods—“optimal coordinates” (Raîche et al., 2013), “parallel analysis” (Horn, 1965), and “comparison data” (Ruscio & Roche, 2012)—which were the 3 best-performing methods in Ruscio & Roche’s (2012) comparative analysis of methods for selecting number of factors. All of these methods indicated that retainment of 3 factors was optimal. A multivariate Shapiro-Wilk test for normality indicated that the Chinese data were not normally distributed ($W = 0.885, p < 0.0001$), so following the recommendation of Costello & Osborne (2005), I employed the principal axis factoring method. Although the data were not normal, they did satisfy both the Kaiser-Meyer-Olkin criterion ($KMO = 0.87$) and Bartlett's test for sphericity ($\chi^2(630) = 3358.62$; $p < .001$), where each of these results indicates adequacy for factor analysis. For factor rotation I followed Roebuck & Lupyan (2020), who used oblique factor rotation due to factor correlations, and employed oblimin, a standard method for oblique rotation.

The extracted factor structure had similarities with the original IRQ factors but also notable differences, and the factor loadings were low overall compared to the original US study (**Table 5.6**). The low factor loadings are likely to be partly due to a difference in procedure between this study and Roebuck and Lupyan (2020)—while the original study progressively narrowed down the number of questionnaire items from 81 to 36 based on their factor loadings and correlations with other items, the present study started with this finalized set of 36 items. The initial, full set of statements would have been more appropriate for the present analysis, but the decision to conduct an exploratory factor analysis was made only after all data were collected. So the exploratory factor analysis was conducted under the limitation of working with the original 36 items that were selected on the basis of a data set from a different population. Alternatively, the factor loadings may be low because of characteristics of response patterns of Chinese participants to statements about internal representation, or due to noise that was introduced during translation, for example. At present, there is no particular reason to believe that there was any problem with the translations.

Because the factor loadings were low, I set the item loading cutoff to ±0.3. This cutoff is more lenient than Roebuck and Lupyan's criterion of ±0.4 and more lenient than common recommendations for exploratory factor analysis, but it is also consistent with some recommendations (e.g., Costello & Osborne, 2005). In the present case, a cutoff of ±0.3 greatly enhances interpretability of the factors, which allows for a more meaningful comparison of the factor structure extracted from the Chinese data to the factor structure from the original US sample.

Following the methodology of Roebuck & Lupyan (2020), I excluded any items whose factor loading exceeded the cutoff on more than one factor, and also dropped any items whose removal increased internal consistency (i.e., Cronbach's alpha) for the factor that it loads on. The final factor structure after this procedure is implemented is shown in **Table 5.7**, and the items in their original English rendition with both their US and Chinese factor names are given in **Table 5.9**.

Table 5.6: Factor loadings of the 3-factor exploratory factor analysis with the Chinese data. The column labeled "R&L factor" indicates the corresponding factor for that item in the original study by Roebuck & Lupyan (2020). h2 indicates communality, and u2 indicates uniqueness, the complement of communality. "Drop" indicates whether the item was dropped from the final factor structure on the basis of the criteria noted in the text.

Item	R&L factor	Factor 1	Factor 2	Factor 3	h^2	u^2	drop
1	Visual	-0.02	0.38	-0.01	0.14	0.86	no
2	Visual	0.06	0.32	0.18	0.19	0.81	no
3	Visual	0.14	0.37	0.14	0.25	0.75	no
4	Visual	0.29	0.12	0.12	0.17	0.83	yes
5	Visual	0.00	0.32	-0.03	0.10	0.90	no
6	Visual	0.02	0.48	0.01	0.24	0.76	no
7	Visual	0.18	0.10	-0.06	0.05	0.95	yes
8	Visual	0.14	0.25	-0.02	0.11	0.89	yes
9	Visual	0.28	0.30	0.05	0.25	0.75	no
10	Visual	0.45	-0.32	-0.19	0.22	0.78	yes
11	Verbal	0.34	0.31	-0.02	0.29	0.71	yes
12	Verbal	0.38	0.20	-0.04	0.23	0.77	no
13	Verbal	0.34	0.20	-0.16	0.19	0.81	no
14	Verbal	0.06	0.43	-0.06	0.20	0.80	no
15	Verbal	0.45	0.06	0.00	0.23	0.77	no
16	Verbal	0.33	0.23	-0.03	0.22	0.78	no
17	Verbal	0.31	0.28	-0.11	0.22	0.78	no
18	Verbal	0.21	0.41	0.12	0.33	0.67	no
19	Verbal	-0.26	0.44	0.03	0.18	0.82	no
20	Verbal	0.51	-0.05	0.01	0.24	0.76	no
21	Verbal	0.28	0.24	-0.09	0.17	0.83	yes
22	Verbal	0.28	0.27	0.05	0.23	0.77	yes
23	Orthographic	0.65	-0.05	0.14	0.45	0.55	no
24	Orthographic	0.31	0.24	0.03	0.22	0.78	no
25	Orthographic	0.54	-0.02	0.03	0.29	0.71	no
26	Orthographic	0.43	0.03	0.08	0.23	0.77	no

27	Orthographic	0.52	0.11	0.05	0.34	0.66	no
28	Orthographic	0.27	0.13	0.06	0.13	0.87	yes
29	Manipulation	0.09	0.00	0.73	0.56	0.44	no
30	Manipulation	0.37	0.08	0.17	0.24	0.76	no
31	Manipulation	0.07	-0.03	0.61	0.39	0.61	no
32	Manipulation	0.04	0.09	0.24	0.09	0.91	yes
33	Manipulation	-0.14	0.00	0.62	0.37	0.63	no
34	Manipulation	0.27	0.18	0.24	0.26	0.74	yes
35	Manipulation	0.17	0.13	0.22	0.14	0.86	yes
36	Manipulation	0.01	0.19	0.29	0.16	0.85	yes
Variance explained		0.11	0.07	0.05			

Table 5.7: Factor loadings for the factor structure given by the exploratory factor analysis, after items have been dropped. Factor loadings below the cutoff of 0.3 have been removed for ease of interpretation. The IRQ_factor column indicates the corresponding factor in the original study by Roebuck & Lupyan (2020). Factor 1 is dubbed the "ortho-verbal" factor; Factor 2 is dubbed the "visuo-verbal" factor; Factor 3 is dubbed the "spatial manipulation" factor, see text.

Item	IRQ factor	Factor 1	Factor 2	Factor 3
1	Visual		0.38	
2	Visual		0.32	
3	Visual		0.37	
5	Visual		0.32	
6	Visual		0.48	
9	Visual		0.30	
12	Verbal	0.38		
13	Verbal	0.34		
14	Verbal		0.43	
15	Verbal	0.45		
16	Verbal	0.33		
17	Verbal	0.31		
18	Verbal		0.41	
19	Verbal		0.44	
20	Verbal	0.51		
23	Orthographic	0.65		
24	Orthographic	0.31		
25	Orthographic	0.54		
26	Orthographic	0.43		
27	Orthographic	0.52		

29	Manipulation			0.73
30	Manipulation	0.37		
31	Manipulation			0.61
33	Manipulation			0.62

Extracted factor structure

Factor 1 was loaded on by many of the items that were coded as internal verbalization in the original IRQ study, but it also includes the orthographic imagery items, suggesting that these two modalities are not statistically separable in the Chinese population[23]. One of the items coded as representational manipulation in the original study also loaded onto Factor 1, perhaps appropriately as it was an item that concerned the verbal modality[24].

Factor 2 was the only factor that was loaded on by visual imagery items, and thus appears to primarily be a visual factor, although there were a number of items coded as internal verbalization that also loaded on this factor. Tentatively, the splitting of internal verbalization items between Factors 1 and 2 may be occurring along the lines of discursive vs. non-discursive items (Alderson-Day et al., 2018; McCarthy-Jones & Fernyhough, 2011), where items with a discursive or reasoning-like quality load onto Factor 1 (e.g., item 15, "I tend to think things through verbally when I am relaxing") whereas items that lack an explicit reasoning-like component (e.g., item 14, "My inner speech helps my imagination") load onto Factor 2. There is not enough information in the present analysis to substantiate this hypothetical structure, and it will require further study.

Factor 3 comprised only 3 items but with high loading. These items were all from the representational manipulation factor, and they were a subset that specifically concerned spatial manipulation of geometric constructs. The other items in the original representational manipulation factor pertained to other, non-spatial modalities—in particular verbal, gustatory,

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[23] This merging of the internal verbalization and orthographic imagery items was also observed in an informal exploratory factor analysis of the Japanese sample, whose results are not described here due to the problem of limited sample size as noted above

[24] Item 34, "I can easily imagine someone clearly talking, and then imagine the same voice with a heavy cold"

and auditory representations[25], so this factor appears to be strictly selective for spatial manipulation.

The intercorrelations of the factors for this exploratory factor analysis (**Table 5.8**) were substantially lower than the intercorrelations in the confirmatory factor analysis (**Table 5.5**), suggesting that the new factors were comparatively well-separated. Internal reliability was reasonably good, and at a similar level to the confirmatory factor analysis (**Table 5.8**).

In sum, although the factor loadings were lower in the present analysis than they were in the original study by Roebuck and Lupyan (2020), several unique findings emerged: (1) A large portion of the items concerning internal verbalization loaded onto the same factor as the orthographic imagery items. These verbal items may have in common a discursive or reasoning-like component. (2) The visual imagery items clustered together, although they were also associated with a number of items related to internal verbalization that may be defined by their absence of the discursive component noted above. (3) Spatial manipulation of geometric constructs constituted its own factor. To encapsulate these provisional findings, I will label Factor 1 as the "ortho-verbal" factor, Factor 2 as the "visuo-verbal" factor, and Factor 3 as the "spatial manipulation" factor (**Table 5.7**), although the validity of these constructs is not yet clear without at least a confirmatory factor analysis on a separate sample from the same population. A comparison of the factor labels from the original US study and the new factor labels provided in the present analysis is given in **Table 5.9**. Finally, the intercorrelations revealed that these extracted factors were much better separated than the IRQ factors as tested in the confirmatory factor analysis, and internal reliability was mostly adequate (**Table 5.8**).

Table 5.8: Factor intercorrelations and internal reliability. Cronbach's alpha are for values after items were dropped according to the criterion noted in the text

Factor	1	2	3	α
1	~			0.79
2	0.38	~		0.66
3	0.24	0.28	~	0.71

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[25] A clean separation between spatial manipulation of geometric constructs and non-spatial manipulation of other modalities was also observed informally in exploratory factor analysis of the Japanese data.

Table 5.9: IRQ items with factor labels from both the original US study and the exploratory factor analysis in the original study. Items 19 and 33 were reverse-coded. Blank cells in the Chinese factor column are items that were dropped based on the procedure described in the text.

Item	US factor	Chinese factor	Statement
1	visual	visuo-verbal	I often enjoy the use of mental pictures to reminisce
2	visual	visuo-verbal	I can close my eyes and easily picture a scene that I have experienced
3	visual	visuo-verbal	My mental images are very vivid and photographic
4	visual		The old saying “A picture is worth a thousand words” is certainly true for me
5	visual	visuo-verbal	When I think about someone I know well, I instantly see their face in my mind
6	visual	visuo-verbal	I often use mental images or pictures to help me remember things
7	visual		My memories are mainly visual in nature
8	visual		When traveling to get to somewhere I tend to think more visually than verbally
9	visual	visuo-verbal	If I talk to myself in my head it is usually accompanied by visual imagery
10	visual		If I imagine my memories visually they are more often static than moving
11	verbal		I think about problems in my mind in the form of a conversation with myself
12	verbal	ortho-verbal	If I am walking somewhere by myself, I often have a silent conversation with myself
13	verbal	ortho-verbal	If I am walking somewhere by myself, I frequently think of conversations that I’ve recently had
14	verbal	visuo-verbal	My inner speech helps my imagination
15	verbal	ortho-verbal	I tend to think things through verbally when I am relaxing
16	verbal	ortho-verbal	When thinking about a social problem, I often talk it through in my head
17	verbal	ortho-verbal	I like to give myself some down time to talk through thoughts in my mind
18	verbal	visuo-verbal	I hear words in my "mind’s ear" when I think
19	verbal	visuo-verbal	I rarely vocalize thoughts in my mind*
20	verbal	ortho-verbal	I often talk to myself internally while watching TV
21	verbal		My memories often involve conversations I’ve had
22	verbal		When I read, I tend to hear a voice in my "mind’s ear"
23	orthographic	ortho-verbal	When I hear someone talking, I see words written down in my mind
24	orthographic	ortho-verbal	I see words in my "mind’s eye" when I think
25	orthographic	ortho-verbal	When I am introduced to someone for the first time, I imagine what their name would look like when written down
26	orthographic	ortho-verbal	A strategy I use to help me remember written material is imagining what the writing looks like
27	orthographic	ortho-verbal	I hear a running summary of everything I am doing in my head
28	orthographic		I rehearse in my mind how someone might respond to a text message before I send it
29	manipulation	spatial manipulation	I can easily imagine and mentally rotate three-dimensional geometric figures
30	manipulation	ortho-verbal	I can easily choose to imagine this sentence in my mind pronounced unnaturally slowly
31	manipulation	spatial manipulation	In school, I had no problems with geometry
32	manipulation		It is easy for me to imagine the sensation of licking a brick
33	manipulation	spatial manipulation	I find it difficult to imagine how a three-dimensional geometric figure would exactly look like when rotated*
34	manipulation		I can easily imagine someone clearly talking, and then imagine the same voice with a heavy cold

35	manipulation		I think I have a large vocabulary in my native language compared to others
36	manipulation		I can easily imagine the sound of a trumpet getting louder

Association of factor scores with participant characteristics

Using the factor structure extracted by the exploratory factor analysis, I computed factor scores for each participant in the Chinese sample. A factor score is a weighted average of a participant's responses across the items that measure a given factor, and is a more accurate measure of the participant's placement on that factor than simple sum scores of observed responses. In order to gain further insight into the participant characteristics of the Chinese sample that explain variation in internal representations, I conducted a multiple regression analysis with demographic variables as predictors and factor scores as outcomes (**Table 5.9**). Age and time spent reading were log-transformed due to a heavy positive skew in each, and all variables were standardized except for gender. For identification of gender we offered participants the options "male", "female", and "other", but all of them selected male or female, rendering the variable dichotomous. There was one participant who was excluded from this part of the analysis due to their years of education being reported as 49.

Table 5.10: Regression analyses using demographic and background variables of the Chinese participants to predict their factor scores across the 3 factors extracted above from the exploratory factor analysis. All variables other than gender are standardized, and age and dense reading are log-transformed. Gender is dichotomous, and coded as 1=male, 2=female.

	Ortho-verbal				Visuo-verbal				Spatial manipulation			
	β	SE	*t*	*p*	β	SE	*t*	*p*	β	SE	*t*	*p*
English usage	0.03	0.05	0.64	0.520	0.07	0.05	1.31	0.190	0.12	0.05	2.15	0.032
English thinking	0.29	0.05	5.57	<0.001	0.17	0.05	3.23	0.001	0.09	0.05	1.80	0.072
Dense reading	0.11	0.04	2.88	0.004	0.13	0.04	3.26	0.001	0.10	0.04	2.40	0.017
Age	-0.01	0.04	-0.30	0.765	0.04	0.04	0.97	0.335	0.18	0.04	0.45	0.652
Gender	-0.10	0.08	-1.15	0.251	-0.04	0.08	-0.54	0.587	-0.24	0.08	-3.03	0.003
Education	-0.08	0.06	-1.41	0.158	-0.05	0.06	-0.77	0.439	0.07	0.06	1.23	0.219
R^2	0.153				0.097				0.084			

There was a fairly substantial gender effect for the spatial manipulation factor: male factor scores for spatial manipulation were on average 0.24 standard deviation units higher than females. Although self-report is prone to biases in self-evaluation, this outcome is consistent with the widely replicated finding that males have an advantage over females in spatial cognition tasks such as mental rotation (Levine et al., 2016). For factor scores across all 3 factors, there was a positive effect of the reported (log-transformed) hours per week spent on dense reading (e.g., on books and newspapers rather than social media). Moreover, the magnitude of association was roughly equal across the 3 factors (ortho-verbal, β=.11; visuo-verbal, β=0.13; spatial manipulation, β=0.10), suggesting that reading is associated with the self-perceived strength of internal representations regardless of modality.

In this regression I included two variables designed to index the participant's immersion in the English language. One is English thinking, which encodes Likert responses to a Chinese statement that corresponds to, "I frequently think in English." The other is English usage, which similarly encodes Likert responses but to a statement that corresponds to "I frequently use English in daily life (such as reading English texts, watching English films, engaging in English conversations, etc.)." English thinking and English usage are highly correlated (Pearson's r = 0.66), but their variance inflation factors are sufficiently low (English thinking, VIF = 1.81; English usage, VIF = 1.86), suggesting that collinearity is not an immediate problem.

For the ortho-verbal (Factor 1) and visuo-verbal (Factor 2) factors, factor scores were predicted by English thinking (ortho-verbal, $\beta=0.29$, $p<.001$; visuo-verbal, $\beta=.17$, $p<.001$) but not English usage (ortho-verbal, $\beta=0.03$, $p=0.52$; visuo-verbal, $\beta=.07$, $p=0.19$). English thinking may be predicting ortho-verbal and visuo-verbal scores simply by functioning as additional measurement items of these latent factors—a suspicion that is supported by a test of internal reliability[26]. Under this scenario, "I frequently think in English" may just be another statement about internal verbalization in general, and the fact that the statement concerns the English language in particular may be immaterial. In contrast to the other two factors, spatial manipulation (Factor 3) was associated with a weak and marginally non-significant effect of English thinking ($\beta=.09$; $p=.072$), and a similar albeit significant effect of English usage ($\beta=.12$; $p=.032$).

When the same regression was conducted without English thinking, English usage predicted factor scores with roughly equal magnitude across the three factors (ortho-verbal, $\beta=.22$; visuo-verbal, $\beta=.18$; spatial manipulation, $\beta=.18$; all $p<0.01$), thereby suggesting that English usage, like reading, is associated with the strength of internal representations in general, regardless of modality. Therefore, for the ortho-verbal and visuo-verbal factors, the effect of English usage is masked by English thinking, where the latter may in fact be functioning just as a measurement item of these factors.

In sum, the analysis of factor scores revealed an effect of gender for the spatial manipulation factor, and what plausibly appear to be general effects of reading and English usage across all three factors, despite the masking of English usage by English thinking in the ortho-verbal and visuo-verbal factors. The impact of English immersion (thinking and usage) on factor scores is not yet clear.

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[26] For the ortho-verbal factor, Cronbach's alpha slightly increased from 0.79 to 0.80 when English thinking was included as a measurement item, and remained constant when English usage was instead included; for the other two factors, inclusion of either English thinking or usage led to a slight reduction.

Discussion

Cultural psychology has revealed substantial cross-cultural variation in perceptual processing, particularly for the visual modality, as well as the correspondence of such perceptual traits with other cultural variables such as social interdependence–independence (Kitayama et al., 2009). This body of research has supplied compelling evidence that the organization of the human mind is permeable to cultural influence, working against the classical cognitivist viewpoint that emphasizes the universality and invariance of the human mind. One weakness of this paradigm however has been its inflated focus on analytic–holistic cognitive style at the expense of other possible dimensions of variation. Another weakness has been its relative paucity of inquiry into individual differences within cultures.

To extend the standard approach, I employed the recently developed Internal Representations Questionnaire (IRQ; Roebuck & Lupyan 2020). The IRQ is an instrument to probe individual differences in modalities of thought. Its items are designed to uncover the modal structure of mental representations, and is hence built according to a different philosophy from that of analytic–holistic cognitive style. Whereas the analytic–holistic continuum examines how information given in the perceptual field is processed and internally represented as an outcome of how attentional and perceptual resources are arranged, the IRQ examines variation in the qualitative structure of the perceptual field itself (including offline sensorimotor representations): the representational formats in which information is presented in the first place. To employ a loose metaphor, analytic–holistic cognitive style describes the compression method used to transmit a given data format such as an image, while the IRQ evaluates the characteristics of the data format itself—whether the information is delivered as image, movie, voice message, or interactive program.

Although there is a large body of research on variation in modalities of thinking such as the visualizer–verbalizer continuum (Kirby et al., 1988; Mayer & Massa, 2003), the IRQ is a unique, bottom-up approach to the investigation of representational format that follows different assumptions. In a US sample, the IRQ has revealed a novel factor structure that contained theoretically unexpected components. By administering the questionnaire to cultural populations that were different from the original study, I investigated both cross-cultural and within-culture individual differences in internal representation. In particular, I studied people in Japan and the People's Republic of China, under the hypothesis that variation in writing systems may account for meaningful variation in internal representations across cultures.

Summary of outcomes

A simple comparison of raw and standardized scores using the factor structure extracted from the US sample in the original study (Roebuck & Lupyan, 2020) revealed substantive differences between cultures (**Table 5.1**; **Figure 5.2**). After implementing within-culture standardization to reduce the effect of culture-specific response styles (Fischer, 2004), Chinese and Japanese scores were considerably higher than US scores on the orthographic imagery factor, and US scores were higher than Chinese and Japanese scores on the internal verbalization factor. There were other cross-cultural differences as well, including between the Chinese and Japanese samples, but the magnitude of these findings were smaller.

In my preregistration prior to collecting the Chinese data, I had predicted that the Chinese scores for orthographic imagery would be similar to or higher than the Japanese scores for the same IRQ factor, and that the Chinese scores for internal verbalization would be similar to or lower than the Japanese scores for the same factor. This was based on an earlier observation, prior to the Chinese preregistration, that Japanese participants reported higher orthographic imagery and lower internal verbalization compared to the US participants. The inference drawn from this finding was that internal representations of the Chinese group should take an even more pronounced form of this cultural contrast, due to written Chinese being an almost pure logographic system, while written Japanese combines a logographic system that is a variant of the Chinese system with two phonetic systems that are relatively closer to the English alphabet. The expected pattern was that logographic writing systems promote orthographic imagery while phonetic writing systems promote internal verbalization.

In the standardized comparison (**Figure 5.2, bottom**), the prediction about Chinese scores for orthographic imagery was realized. The prediction about internal verbalization was strictly speaking rejected, as mean internal verbalization scores were smaller in the Chinese sample than they were in the Japanese sample, but the difference between the Chinese scores and the Japanese scores was only 0.02 standard scores, and statistical evidence for the difference was significant but weak. These simple comparisons therefore indicated cross-cultural differences in the structure of internal representations that are consistent with the properties of their respective writing systems.

It remained unclear whether the original factor structure of Roebuck and Lupyan (2020), derived from their US sample, was a good fit for the Chinese and Japanese data. A confirmatory factor analysis yielded mixed results, due to ambiguous goodness-of-fit measures and factor intercorrelations in the Chinese and Japanese data, which were considerably higher than in the US data. I therefore conducted an exploratory factor analysis with the Chinese data but not the Japanese data, due to a limitation in sample size for the latter. The analysis revealed a 3-factor structure: (1) an "ortho-verbal" factor that comprises orthographic imagery as well as some internal verbalization items that may have in common a discursive character, (2) a "visuo-verbal" factor that comprises visual imagery as well as some internal verbalization items that may have in common a non-discursive character, and (3) a "spatial manipulation" factor that is a subset of the representational manipulation factor of the original IRQ study, containing items related to the manipulation of geometric objects but excluding other modalities of representational manipulation. The exploratory factor analysis was methodologically constrained by being limited to the 36 items that comprise the IRQ—these items were selected from a larger pool of 81 items during the construction of the questionnaire, in accordance with the patterns discovered among the US respondents. A more robust method for conducting the exploratory factor analysis would start with a larger, unconstrained set of items that hasn't been pared down in this manner.

Using the extracted 3-factor structure to further analyze the Chinese data, a comparison of factor scores with demographic variables revealed a number of findings. Higher scores were observed across all 3 factors among individuals who reported more time spent reading, as well as individuals who reported greater levels of immersion in the English language (i.e., English thinking or English usage). This may indicate that engagement with linguistic material—whether in the form of immersion in a foreign language or in reading—is associated with more vivid internal representations overall. Roebuck and Lupyan (2020) had also found that mean responses across factors correlate with each other, instead of being organized as a tradeoff between different factors, although research on cognitive styles such as the visualizer–verbalizer continuum often assumes a tradeoff between styles (e.g., Mayer & Massa, 2003). It is also possible that the present outcome reflects response bias—resolution of these findings will require further investigation. Males had higher factor scores on the spatial manipulation factor than females, as predicted based on a large body of past research, and a gender effect was present only for this one factor.

Interpretation of the Chinese factors

The factor structure extracted from the Chinese sample differed from the factor structure reported by Roebuck and Lupyan (2020) for their US sample. Although confirmation of this factor structure requires further study, the structure revealed here may serve to point us toward qualitative differences in the organization of internal representations between Chinese and US individuals. All 3 of the employed selection methods converged upon a 3-factor structure. Two of the extracted factors joined items across the US factors: items pertaining to orthographic imagery were merged with a subset of internal verbalization items (the "ortho-verbal" factor), while items pertaining to visual imagery were merged with a different subset of internal verbalization items (the "visuo-verbal" factor). The representational manipulation factor of the US study was not recovered in its original form, but a subset of the items pertaining specifically to mental rotation of geometric objects formed the third factor (the "spatial manipulation" factor).

Ortho-verbal conjunction

The joining of orthographic imagery and internal verbalization mirrors the postulation by Perfetti et al. (2013) that English reading involves extensive conversion of visuo-orthographic input into phonological representations, while Chinese reading involves more sustained activation of both orthographic and phonological representations. This is ultimately due to a structural property of Chinese characters, namely how they primarily encode semantic meaning and only subordinately phonemic information, in contrast to the more direct phonological encoding of alphabetic characters.

In Chinese orthography, tens of thousands of units of meaning are each represented with a dedicated character, and this large array is in turn mapped onto a much narrower set of several hundred toned syllables. This is unlike in English, where isolated graphemes usually do not represent meaning in themselves, but only sounds. The “degenerate” mapping of a large set of characters to a smaller set of sounds in Chinese orthography results in a high density of homophony, where a single phoneme commonly maps onto multiple mutually exclusive characters, and hence meanings. This ambiguity induced by dense homophony promotes the development of a direct route of cognitive access from orthography to meaning that is unmediated by phonology. This direct access requires sustained activation of visuo-orthographic representations in parallel with phonological representations (Perfetti et al., 2013).

Neuroimaging studies show that a comparison of Chinese- and English-reading children demonstrates developmental divergence in their cortical responses to orthographic input. These data suggest that sustained activation of visuo-orthographic representations in Chinese readers is subserved by cortical regions such as the superior parietal lobule, the inferior temporal gyrus, and the middle occipital gyrus, all of which are areas involved in visuo-orthographic analysis (Cao et al., 2009, 2010, 2014). This neurocognitive divergence occurs as an outcome of the different properties of the two writing systems, and potentially explains the discrepancy between the orthographic imagery factor that was extracted from the US sample by Roebuck and Lupyan (2020) and the composite ortho-verbal factor that was extracted from the Chinese sample in the present study. For the Chinese sample, there was no statistical separation between orthographic imagery and at least some components of internal verbalization, suggesting a tighter coupling between these two modalities of representations compared to the US sample.

The IRQ was designed to investigate how individual differences in the structure of mental representations may influence cognitive function and behavior more broadly. Roebuck and Lupyan (2020) argue that given the categorical and compositional properties of linguistic representation, individuals with a greater tendency or capacity to deploy internal verbalization may be able to leverage this "interface" to engage with the world through a more categorical or compositional cognitive stance (Lupyan, 2012; Lupyan & Bergen, 2016). Such a stance may be useful or undesirable depending upon the goal.

If the above account regarding the direct pathway from orthographic input to semantic meaning among the Chinese is correct, it may indicate the possibility that for people trained natively in Chinese orthography, a categorical or compositional interface with the world can be deployed with a relatively small reliance (or no reliance) or internal verbalization. Rather than being primarily mediated by an inner voice that is adjacent to auditory and vocal-motor modalities, as it presumably would be in English-readers, for Chinese-readers the language-augmented interface would instead be mediated by orthographic imagery that is adjacent to spatial vision and manual-motor skill. There is evidence that in Chinese children, visual ability (Koyama et al., 2011; Yang et al., 2013) and manual writing skill (Tan, Spinks, et al., 2005) predict reading skill better than they do in Western children. Moreover, acquisition of literacy may play a causal role in the improvement of visual ability in Chinese-reading children (Demetriou et al., 2005; McBride-Chang et al., 2011). Such findings suggest that different writing systems offer different opportunities and constraints for shaping neurocognitive development, perhaps simply as a consequence of the material (e.g., geometric, statistical, distributional) properties of their constituent symbols. Further cultural differences could build upon these neurocognitive trajectories to drive further divergence.

Discursive vs. non-discursive verbalization

It is not self-evident why the internal verbalization-related items subsumed by the ortho-verbal factor appear to share a discursive character. However, previous research using the Varieties of Inner Speech Questionnaire (VISQ and VISQ-R) found that self-reports about inner speech can be decomposed into multiple factors, one of which is a factor for "dialogic" inner speech (Alderson-Day et al., 2018; McCarthy-Jones & Fernyhough, 2011) that overlaps considerably with the discursive items that loaded onto the ortho-verbal factor in the Chinese sample. This proposed sub-division of internal verbalization is consistent with the factor structure extracted in the present study. It also means that it may be possible in a future study to use items from the VISQ to distinguish between dialogic and non-dialogic items, and explore the robustness of the apparent separation of these items in the extracted factor structure.

If internal representations of orthographic symbols are directly linked to atomic units of semantic meaning among Chinese-readers (through the direct pathway discussed above), then it is plausible that in the same population, internal representations of higher-order ortho-visual structures such as sentences or narratives are directly linked to higher-order units of meaning such as discourse. For English-readers, the same input in their native script would be more immediately tied to internal verbalization, and the link to discursive meaning would be mediated by this modality. On this scenario, Chinese readers would be able to comprehend discursive text with less reliance on internal verbalization, whereas discursive text for English readers is obligatorily tied to internal verbalization. Discursive items may be occupying the same factor as orthographic items in the Chinese factor structure as a downstream consequence of this immediacy. If this were the case, the factor label "ortho-verbal" that I employ here would potentially be misleading, as the internal representation of discourse would in fact be non-verbal in character.

The visuo-verbal factor also subsumed a number of items that were associated with internal verbalization in the original US study. These items appeared to have in common a lack of the discursive component. Speculatively, they may pertain more to the immediate sensation or action of vocalization, rather than discourse, but the number of these items was too small to allow any measured judgment of their collective properties. One of these items, item 14 ("My inner speech helps my imagination"), carries an implicit connection to the visual modality insofar as imagination is commonly construed visually, but the other two do not do so in any obvious manner. It is not clear why visual imagery would be merged with internal verbalization, whether discursive or not, nor whether this is a robust finding in the first place. The organization of this factor will require further study.

Spatial manipulation

The representational manipulation factor of Roebuck and Lupyan (2020) was reduced to a subset pertaining specifically to spatial manipulation, but it was not clear why this should be the case. The coherence of this subset was strong, with the items loading on this spatial manipulation factor having the highest factor loadings among all the questionnaire items. We may predict that some component of the Chinese cultural environment, such as the educational curriculum, tends to decouple spatial manipulation from other modalities of representational manipulation when compared to the US population, although little is clear.

Conclusion

Administering the Internal Representations Questionnaire (IRQ) in Chinese and Japanese samples, I was able to obtain preliminary evidence regarding cross-cultural differences in the structure of internal representations. These populations were appropriate for testing the hypothesis that variation in writing systems induces variation in internal representations. A naive comparison of item responses using the factor structure extracted from the original US study demonstrated that respondents from the two east Asian cultures gave higher scores for orthographic imagery and lower scores for internal verbalization compared to respondents from the US sample, a finding that meshes with basic features of their respective writing systems. A confirmatory factor analysis raised doubt about whether the US factors were appropriate for the two new samples, so I performed an exploratory factor analysis on the Chinese data, and extracted a 3-factor structure that differed non-trivially from the US factor structure. There were methodological constraints in this analysis, but the extracted factor structure suggested differences in the organization of internal representations between Chinese and US participants, revealing findings that are partly consistent with data from cross-cultural studies on cognitive development and neuroimaging. In particular, some components of internal verbalization—possibly of a discursive character—were statistically inseparable from orthographic imagery, suggesting that these two domains of ability are closely tied together in Chinese but not US participants. This may be a downstream consequence of differences in the material properties of the two writing systems, a scenario that if true would reveal the potency of cultural transmission in shaping fundamental aspects of human psychology.

Appendix

Below:

- **Document 5.1** (pp. 182–187)

  Document preregistered for Japanese sample, following the format of aspredicted.org (6 pages); uploaded to {https://osf.io/nxmg2/} on 16 July 2020

- **Document 5.2** (pp. 188–195)

  Document preregistered for Chinese sample, following the format of aspredicted.org (8 pages); uploaded to {https://osf.io/nxmg2/} on 28 January 2021

Pre-registration for the Internal Representations Questionnaire administered to a Japanese sample

Created 16 July 2020 by Ryutaro Uchiyama (London School of Economics), following the format of AsPredicted.org:

1) **Data collection. Have any data been collected for this study already?**

Currently being collected by an survey management company, details below.

2) **Hypothesis. What's the main question being asked or hypothesis being tested in this study?**

Can the results of the Internal Representations Questionnaire, originally tested on an American sample, be reproduced in a Japanese sample? If not, do the differences in results reflect any interesting cultural differences?

3) **Dependent variable. Describe the key dependent variable(s) specifying how they will be measured.**

Responses on a Japanese translation of the Internal Representations Questionnaire: Roebuck, H. & Lupyan, G. (2020). The Internal Representations Questionnaire: Measuring modes of thinking. Behavior Research Methods. https://doi.org/10.3758/s13428-020-01354-y/

4) **Conditions. How many and which conditions will participants be assigned to?**

A single survey for all respondents

5) **Analyses. Specify exactly which analyses you will conduct to examine the main question/hypothesis.**

Same analysis as reported in Roebuck & Lupyan (2020)

6) **Outliers and Exclusions. Describe exactly how outliers will be defined and handled, and your precise rule(s) for excluding observations.**

Participants who fail either of the two attention checks, by answering anything other than "strongly agree" (非常に同意できる) or "agree" (同意できる) will be excluded from the analysis. If there are any incomplete outcomes where not all questions have been answered, these will also be excluded. Respondents who provide the identical response across all questions will be excluded as well.

7) Sample Size. How many observations will be collected or what will determine sample size?

115 participants aged between 20 and 72, inclusive (the age range of the participants in the original English-language questionnaire as reported in Roebuck & Lupyan 2020). Sample size was determined by available budget.

8) Other. Anything else you would like to pre-register?

The questions used in the survey were taken from Table 2 of Roebuck & Lupyan (2020), and translated into Japanese by Ryutaro Uchiyama. The survey is being sent out by the Japanese internet research firm Fastask (https://www.fast-ask.com/) to Japanese-speakers living in Japan who are registered in their respondent pool. The survey is being sent out at the time of this pre-registration, and no results have been observed yet.

The order of questions was randomized for each respondent, and included two attention checks. The attention checks were originally translated based on the ones indicated in Roebuck & Lupyan (2020), but one of the questions needed to be revised due to a request by the company, who do not allow for questions that are obvious foil questions. The translated questions are as follows:

1
記憶を楽しく回想するときは、その記憶のイメージや映像を思い浮かべることが多い
I often enjoy the use of mental pictures to reminisce

2
目を閉じて、過去に見た風景を容易に思い浮かべることができる
I can close my eyes and easily picture a scene that I have experienced

3
自分の心に思い浮かべたイメージは、鮮明でまるで写真のようである
My mental images are very vivid and photographic

4
「一枚の絵は千の言葉に値する」という格言は、自分にとてもよく当てはまる
The old saying “A picture is worth a thousand words” is certainly true for me

5
知人のことを考えるときは、その人の顔が即座に浮かんでくる
When I think about someone I know well, I instantly see their face in my mind

6
事柄を記憶に留めておくための手段として、心の中のイメージや映像を利用することがよくある
I often use mental images or pictures to help me remember things

7
自分の記憶は主に視覚的である
My memories are mainly visual in nature

8
目的地に向かって移動している最中の自分の思考は、言語的であるよりは視覚的である
When traveling to get to somewhere I tend to think more visually than verbally

9
心の中で自分自身に語りかける際、視覚的なイメージが付随することが多い
If I talk to myself in my head it is usually accompanied by visual imagery

10
自分の記憶を視覚的に思い起こすとき、それは動画よりは静止画に近い場合が多い
If I imagine my memories visually they are more often static than moving

11
何かの問題について考えているときは、心の中で自分自身と会話をするような感覚である
I think about problems in my mind in the form of a conversation with myself

12
一人で歩いているとき、心の中で自分自身と会話をすることがよくある
If I am walking somewhere by myself, I often have a silent conversation with myself

13
一人で歩いているとき、最近あった人との会話を思い出すことがよくある
If I am walking somewhere by myself, I frequently think of conversations that I’ve recently had

14
心の内部の「声」が自分にとって想像力の手助けになる
My inner speech helps my imagination

15
リラックスしているときの思考は言語的であることが多い
I tend to think things through verbally when I am relaxing

16
社会問題について考えるときは、その内容をじっくりと頭の中で語ることが多い
When thinking about a social problem, I often talk it through in my head

17
休息をとりながら、考え事をじっくりと頭の中で言い表すことを好む

18
思考するとき、心の中の「耳」で言葉を聴きとる感覚である
I hear words in my "mind’s ear" when I think

19
思考するとき、その思考内容を心の中で「発声」する感覚は普段特に無い
I rarely vocalize thoughts in my mind

20
テレビを見ているとき、心の中で独り言を言うことがよくある
I often talk to myself internally while watching TV

21
記憶を想起するときは、過去の会話の記憶であることが多い
My memories often involve conversations I’ve had

22
文章を読むときは、心の中の「耳」で朗読を聞く感覚である
When I read, I tend to hear a voice in my "mind’s ear"

23
人の話を聞くとき、話が文字として心の中に浮かんでくる
When I hear someone talking, I see words written down in my mind

24
思考するとき、その思考内容が心の中の「眼」で文字として見える
I see words in my "mind’s eye" when I think

25
人を初めて紹介されたとき、相手の名前を文字としてイメージする
When I am introduced to someone for the first time, I imagine what their name would look like when written down

26
手書きの文書やメモの内容を思い出そうとするときは、書かれた文字の見た目をイメージすると手助けになる
A strategy I use to help me remember written material is imagining what the writing looks like

27
日常生活の中で、自分の行動を解説する声が心の中で聞こえる感覚がある
I hear a running summary of everything I am doing in my head

28
人にメッセージを送信する前に、それに対する相手の返信をまずイメージする
I rehearse in my mind how someone might respond to a text message before I send it

29
三次元の立体を想像し、それを頭の中で回転させることは容易にできる
I can easily imagine and mentally rotate three-dimensional geometric figures

30
この文を不自然にゆっくりと読み上げる声を頭の中で想像するのは容易である
I can easily choose to imagine this sentence in my mind pronounced unnaturally slowly

31
学校の授業で幾何学は得意だった
In school, I had no problems with geometry

32
レンガを舌で舐める感覚を、容易に想像することができる
It is easy for me to imagine the sensation of licking a brick

33
三次元の立体があるとして、それが回転するとどう見えるのか正確にイメージするのは難しい
I find it difficult to imagine how a three-dimensional geometric figure would exactly look like when rotated

34
誰かがはっきりと喋る音声を想像するのは容易であり、その同じ人が重い風邪を引いたような声で喋る音声も想像できる。
I can easily imagine someone clearly talking, and then imagine the same voice with a heavy cold

35
自分は他の人と比べて、（母国語で）知っている言葉の数は多い方である
I think I have a large vocabulary in my native language compared to others

36
トランペットの鳴っている音が徐々に大きくなっていくのを容易に想像することができる
I can easily imagine the sound of a trumpet getting louder

Attention check 1:
Elephants are larger than dogs
ゾウと犬を比較すれば、ゾウの方が大きい。

Attention check 2:
Giraffes are larger than turtles
キリンと亀を比較すれば、キリンの方が大きい。

Response options
Strongly agree
非常に同意できる
Agree
同意できる
Neither agree nor disagree
どちらともいえない
Disagree
同意できない
Strongly disagree
全く同意できない

Pre-registration for the Internal Representations Questionnaire administered to a Chinese sample

Created 28 January 2021 by Ryutaro Uchiyama (London School of Economics), following the format of AsPredicted.org:

1) **Data collection. Have any data been collected for this study already?**

Not yet. To be collected by a survey management company (details below).

2) **Hypothesis. What's the main question being asked or hypothesis being tested in this study?**

When we ran the Internal Representations Questionnaire (IRQ; Roebuck & Lupyan, 2020) on a Japanese sample, we found that the Japanese sample had a higher mean score on the orthographic factor compared to the original US sample. The Japanese sample also had a lower mean score on the verbal factor compared to the US sample. These differences were found in both the raw scores and scores that were standardizing within-country (a conventional method for adjusting for cross-cultural differences in response biases; Fischer, 2004). We suspect that these differences in reported internal representation between the US and Japanese samples result from differences in writing systems between the two societies, where the US uses an alphabetic system and Japan a mixed logographic and syllabic system. We expect that the logographic component (*kanji*) in particular is driving the difference between the two societies.

Written Chinese is a purely logographic system, and we thus predict a Chinese IRQ profile that is either similar to the Japanese results or even more pronounced along the same dimensions that differentiate the Japanese profile from the US profile, namely, being lower on the verbal factor and higher on the orthographic factor. We will also test the degree to which exposure to written language is associated with exposure to written language: in particular, whether some combination of (1) years of education, (2) hours spent reading per week, and (3) frequency of use of the English language in everyday life mediate the cross-cultural effect. Years of education and hours spent reading per week are predicted to be associated with a lower score on the verbal factor and a higher score on the orthographic factor, whereas use of English is predicted to have an opposite effect due to the phonetic character of the writing system. All three of these variables are expected to be positively correlated with each other.

3) **Dependent variable. Describe the key dependent variable(s) specifying how they will be measured.**

Responses on a Chinese translation of the Internal Representations Questionnaire, with several demographic questions appended (see below).

4) Conditions. How many and which conditions will participants be assigned to?

A single survey for all participants, varying only in the order of the questions.

5) Analyses. Specify exactly which analyses you will conduct to examine the main question/hypothesis.

We will obtain mean factor scores across the 4 IRQ factors for the Chinese sample, and compare these to the factor scores of both the US and Japanese samples. Scores for each factor will be standardized within-country (Fischer, 2004) due to differences in the expected distribution of Likert scale responses between North American and East Asian samples, where East Asians commonly use responses closer to the mid-point (Chen, Lee & Stevenson, 1995; Tasaki & Shin, 2017).

We will compare these scores across cultures using t-tests and mixed-effects models. For the mixed-effects models, we will use factor, country, and their interactions as fixed effects; respondent ID and question number (nested within factor) as random effects; and Likert responses as the outcome variable.

Within the Chinese sample, we will also use a linear regression model to examine whether the background questions, which include degree of English exposure, degree of general exposure to written material, and years of education, are associated with the factor scores. These variables are not present within the US and Japanese data.

6) Outliers and Exclusions. Describe exactly how outliers will be defined and handled, and your precise rule(s) for excluding observations.

Respondents who fail either of the two attention checks, by answering anything other than "strongly agree" (非常に同意できる) or "agree" (同意できる) will be excluded from the analysis. Respondents who provide the same response on 90% or more of the primary questions (i.e., all questions other than consent, demographic, and attention check questions) will also be excluded, due to suspicion of unreflective responding. In the preregistration for the Japanese sample, we had set a less stringent criterion where only identical responses across all questions warranted exclusion. If there are any incomplete submissions where some questions have been left answered, these will be excluded as well.

7) Sample Size. How many observations will be collected or what will determine sample size?

Our budget appears to allow for 480 participants, so we will adopt this sample size unless some unexpected additional cost factors come into play.

8) Other. Anything else you would like to pre-register?

The questions that are to be used in the survey were taken from Table 2 of Roebuck & Lupyan (2020), and translated into Chinese by Gandalf Li. The survey will be sent out by the Chinese survey management company WJX (https://www.wjx.cn/) to a Chinese-literate sample in the People's Republic of China.

The order of questions will be randomized for each respondent. Two attention checks that were translated from Roebuck & Lupyan (2020) are included, as well as a number of demographic questions and questions about language exposure.

The translated questions are as follows:

1
I often enjoy the use of mental pictures to reminisce
我常常喜欢通过脑海中的画面来回忆过去

2
I can close my eyes and easily picture a scene that I have experienced
闭上眼睛，我可以轻松地看见我所经历过的事情的情景

3
My mental images are very vivid and photographic
我脑海中的画面非常生动和真实

4
The old saying "A picture is worth a thousand words" is certainly true for me
有言道"一画抵千言"，这句话用在我身上非常合适

5
When I think about someone I know well, I instantly see their face in my mind
当我想到一个我很熟悉的人，他/她的脸会立刻浮现在我心中

6
I often use mental images or pictures to help me remember things
我经常通过脑海中的画面或者图像去帮助我记住事情

7
My memories are mainly visual in nature
我的记忆在形式上主要是视觉的

8
When traveling to get to somewhere I tend to think more visually than verbally
当我在去往某个地方的路上，我的思考倾向于使用视觉多过使用语言

9
If I talk to myself in my head it is usually accompanied by visual imagery

当我在脑海中和自己对话的时候往往伴随着视觉画面

10
If I imagine my memories visually they are more often static than moving
当我通过视觉去构想记忆中的信息的时候，这些图像更多是静止的而非动态的

11
I think about problems in my mind in the form of a conversation with myself
当我在心中思考问题的时候，我会以和自己对话的形式去思考

12
If I am walking somewhere by myself, I often have a silent conversation with myself
如果我一个人正走在去往某个地方的路上，我往往会和自己进行无声的对话

13
If I am walking somewhere by myself, I frequently think of conversations that I've recently had
如果我一个人正走在去往某个地方的路上，我时常会想到最近刚刚进行过的对话

14
My inner speech helps my imagination
我的心声有助于我的想象力

15
I tend to think things through verbally when I am relaxing
但我在放松的时候我一般会通过语言去想事情

16
When thinking about a social problem, I often talk it through in my head
当我在思考社会问题的时候，我会在脑海中通过语言讲清楚

17
I like to give myself some down time to talk through thoughts in my mind
我喜欢给自己一些闲暇的时间去在脑海中用语言整理思绪

18
I hear words in my "mind's ear" when I think
当我在思考的时候我“心里的耳朵”会听到词语

19
I rarely vocalize thoughts in my mind
我很少在脑海中“读出”我的思想

20

I often talk to myself internally while watching TV
在我看电视的时候我经常在心中自言自语

21
My memories often involve conversations I’ve had
我的记忆往往关于我曾经有过的对话

22
When I read, I tend to hear a voice in my "mind’s ear"
当我在阅读的时候，我“心里的耳朵”会听到一个声音

23
When I hear someone talking, I see words written down in my mind
当我听到别人讲话的时候，我会在脑海中看见被写下来的文字

24
I see words in my "mind’s eye" when I think
当我在思考的时候我“心里的眼睛”会看见词语

25
When I am introduced to someone for the first time, I imagine what their name would look like when written down
当我第一次被介绍给一个人的时候，我会想象出 ta 的名字写下来时候的样子

26
A strategy I use to help me remember written material is imagining what the writing looks like
我会使用想象文字被写下来的样子的方式去帮助自己记住文字信息

27
I hear a running summary of everything I am doing in my head
我会在脑海中听到一个持续的对我正在做的事情的解说

28
I rehearse in my mind how someone might respond to a text message before I send it
在我发出一条信息之前，我会在脑海中预演对方会如何回复

29
I can easily imagine and mentally rotate three-dimensional geometric figures
我可以轻松地在脑海中想象和旋转三维几何形体

30
I can easily choose to imagine this sentence in my mind pronounced unnaturally slowly
我可以轻松地在脑海中想象这个句子正在被奇怪的发音缓慢地阅读

31
In school, I had no problems with geometry
在学校，我学习几何学很轻松

32
It is easy for me to imagine the sensation of licking a brick
对于我来说想象舔一个砖头的感觉很容易

33
I find it difficult to imagine how a three-dimensional geometric figure would exactly look like when rotated
我发现想象一个三维几何形体旋转之后的具体的样子很难

34
I can easily imagine someone clearly talking, and then imagine the same voice with a heavy cold
我可以轻易想象一个人清楚说话的声音，并想象同一个声音得重感冒时候的样子

35
I think I have a large vocabulary in my native language compared to others
和别人相比，我认为我在母语中掌握了很高的词汇量

36
I can easily imagine the sound of a trumpet getting louder
我可以轻松地想象一个喇叭吹得越来越响的声音

Attention Check Questions

37
Elephants are larger than dogs
大象比狗要更大

38
The word ‘hotel’ has three letters
“酒店”这个词包含三个汉字

Response options

Strongly agree
非常同意
Agree
同意

Neither agree or disagree
不同意也不反对
Disagree
不同意
Strongly disagree
非常不同意

Demographic questions

I frequently think in English.
我经常使用英语来思考。

I frequently use English in life (such as reading English texts, watching English films, engaging in English conversations etc.).
我在生活中经常使用英语（如阅读英语文字，看英文电影，进行英语对话等）

How many hours do you spend on dense reading per week? (for example, reading books, newspaper and magazines, papers, long articles etc., light reading such as browsing social media would not count)
您每个星期花在深度阅读上的时间为多少小时？（如阅读书籍、报刊、论文、长文章等，社交媒体浏览、短信息等轻阅读则不算在内）

What is your age?
您的年龄是?

What is your gender identity? (male, female, other)
您的性别认同为?

Counting from the first grade of primary school, how many years of education have you received? (For example, six years of primary school + three years of middle school + three years of high school + four years of undergraduate studies would be 16 years)
从小学一年级算起，您所接受教育的时间为？（例如，小学六年+初中三年+高中三年+本科四年为 16 年）

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Chapter 6: Cultural evolutionary neuroscience

Abstract

Cultural evolution and cultural neuroscience are complementary approaches to understanding the origins and function of cross-cultural differences in psychology. Cultural evolution, and Dual Inheritance Theory more generally, offers a theoretical framework for understanding cultural transmission and cultural change and how these can change gene frequencies. However, these theories have largely ignored the details of the minds engaging in these processes. Cultural evolutionary models tend to treat the brain as a black-box. Cultural neuroscience offers a rich toolkit for examining how cross-cultural psychological differences manifest at a neurological level. However, these tools have largely been used to document differences between populations. Cultural neuroscience tends to ignore why we should expect these differences or how to identify if they are meaningful. We review work in each field to carve a pathway for a productive synthesis. This cultural evolutionary neuroscience will benefit both fields and lead to a more complete understanding of human culture.

Cultural evolution and cultural neuroscience: An opportunity for convergence

Cultural evolution and cultural neuroscience are research programs that cut across traditional disciplinary boundaries and integrate across the biological and social sciences. Both fields try to explain the foundations of human culture, but each draws on different traditions and each relies on different methods, assumptions, and levels of analysis. Although these fields share a common object of inquiry—culture and cultural differences—and although these fields arguably have complementary toolkits, there have been few practical points of contact. In this chapter we hope to sketch out a path toward a productive convergence. To help us understand some of the barriers to this convergence, we'll begin with some history.

Dual Inheritance Theory and the cultural evolutionary framework began as an attempt to describe how natural selection could lead to a propensity to learn from others rather than by oneself and how this in turn could lead to socially transmitted information—culture—emerging as an independent evolutionary system (for a short introduction to cultural evolution, see Chudek, Muthukrishna, & Henrich, 2015; for a review of the history of Dual Inheritance Theory, see Russell & Muthukrishna, 2018). The approach to answering these questions involved developing a series of mathematical models derived from ecology, epidemiology, and population genetics (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). These seminal models described the evolution of social learning and different social learning strategies, how culture and genes could co-evolve, and the long-run consequences of these transmission and filtering processes. Together these models served as a foundation and convincing case for understanding culture as an evolutionary system, where not only genes, but also socially transmitted information could accumulate adaptations to the environment.

Boyd, Richerson, Cavalli-Sforza, and Feldman offered a productive approach and a revolutionary insight, but just as early population genetics models assumed away the messy details of transmission and molecular genetics, so too did these cultural models assume away the messy details of cultural transmission and storage. Current cultural evolutionary models are mostly 'mind-blind', often modeling cultural learning as a process akin to contagion. The actual process of cultural transmission involves the selective transfer of information from one brain to another, and just as the messy details of genetics inform and constrain our understanding of genetic evolution (Casillas & Barbadilla, 2017), understanding the architectural and computational particulars of nervous systems should inform and constrain our understanding of cultural evolution.

Cultural neuroscience is a research program that merged methods from cognitive neuroscience with the theoretical and experimental apparatus of cultural psychology (Chiao, 2009; Han et al., 2013; Kitayama & Uskul, 2011). Cultural psychology initially relied on self-report and qualitative description, but subsequently cultivated a collection of often ingenious behavioral experimental paradigms, for example those reviewed in Nisbett & Miyamoto (2005). But techniques such as fMRI and ERP allowed for a cultural neuroscience and revealed how those cultural differences manifest at a neurological level. For example, researchers have found cross-cultural differences in neural activity when engaging in psychological processes like self-reflection (Chiao et al., 2009; Ma et al., 2014) and empathy (Cheon et al., 2011). There has also been interesting work done on gene–culture interactions, for example the effect of an oxytocin receptor gene on social support-seeking (Kim et al., 2010), of a serotonin transporter gene on individualist–collectivist cultural values (Chiao & Blizinsky, 2010), and of a dopamine receptor gene on independent–interdependent social orientation (Kitayama et al., 2014). These studies guide us toward a better understanding of the neurogenetic and developmental pathways through which culture makes contact with behavior. As a more conceptual contribution, the advent of cultural neuroscience has highlighted the two-way relationship between culture and brains: the expression of culture in individuals must of course be grounded in an underlying neural substrate, but the neural substrate is also shaped by culture, constituting a system of mutual feedback (Kitayama & Salvador, 2017; see also Lehman, Chiu, & Schaller, 2004). Cultural neuroscience makes clear that investigation of culture is incomplete without investigation of the brain.

Cultural neuroscience is an important step in our scientific understanding of culture, but the conceptual and methodological toolkits inherited from cultural psychology and cognitive neuroscience are limited in their ability to account for aspects of culture that are perhaps fundamental. For example, its change over time. Within the cultural evolutionary framework, cultural change—or more specifically, the ability of cultural practices to adapt to the environment (including the social environment) quicker than genes—is central to both the function and origins of human culture. Measuring cultural traits, neurologically or otherwise, offers only a snapshot of an ongoing adaptive process. As such, any insights gained about current cross-cultural differences are incomplete and sometimes difficult to interpret without a general framework of how these traits evolved and their adaptive function at an individual-level, population-level, and the long-run history of their development (Muthukrishna & Henrich, 2019a).

Toward a cultural evolutionary neuroscience

Psychological and behavioral scientists have recently been forced to grapple with the magnitude of psychological differences across societies (Henrich, Heine, & Norenzayan, 2010a; Muthukrishna, Bell, et al., 2018a; Schulz, Bahrami-Rad, Beauchamp, & Henrich, 2018a). Even mental processes often assumed to be universal and hard-wired have been shown to vary cross-culturally. These include low-level visual perception (Nisbett & Miyamoto, 2005), rationality underlying economic decision-making (Henrich et al., 2001), internal representation of conceptual categories (Medin & Atran, 2004), and coding of spatial coordinates (Majid et al., 2004). The malleability of the human mind has been vastly underestimated. Culture runs deep. This underestimation is in large part due to a systematic sampling bias: the vast majority (96%) of experimental participants are people from Western, educated, industrialized, rich, democratic (WEIRD) countries and mostly Americans (68%). Not only is this a narrow slice of human variation, ignoring 88% of the planet, but WEIRD people appear to be extreme on many psychological traits when compared to the full range of global cultural diversity (Henrich, Heine, & Norenzayan, 2010b; Muthukrishna, Bell, et al., 2018b; Schulz, Bahrami-Rad, Beauchamp, & Henrich, 2018). This sampling bias, combined with theoretical foundations that assume an invariant human cognitive architecture (e.g., Neisser, 1967; Newell, 1980), has distorted our estimation of the extent to which culture shapes the mind.

Cultural evolutionary theory postulates that our capacity for complex culture has been the primary driver of our extraordinary success as a species (Henrich, 2016). Culture has shaped the ways in which we interact with our environments, and furthermore, through processes like culture-gene coevolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981), it has also shaped our bodies and brains. The genetic evolution of our anatomy and physiology has progressed in tandem with the cultural evolution of our adaptive knowledge, and the trajectory of human brain evolution sits squarely within this intersection of genetic and cultural evolution (Muthukrishna, Doebeli, et al., 2018b). Cultural practices such as food sharing (Kaplan et al., 2000a), cooking (Wrangham & Carmody, 2010a), midwifery (Rosenberg & Trevathan, 2002), and modern medical interventions (Lipschuetz et al., 2015b) support our large, costly, difficult-to-birth brains, while reciprocally, our enlarged brains support the storage and transmission of more complex cultural knowledge. This process of *brain–culture* coevolution has allowed human cultural complexity to scale up in dramatic ways, and so cultural transmission is intrinsic to the evolutionary and functional history of our nervous systems (Muthukrishna, Doebeli, et al., 2018a; Muthukrishna & Henrich, 2016a).

Here, we take a step further. Rather than a static picture of brain–culture coevolution that only emphasizes the mutual positive feedback between knowledge and brain size (or brain complexity), we will zoom-in on the interaction between two forms of adaptive fluidity: (1) the plasticity of the brain and (2) the intrinsic flexibility of cumulative culture as a dynamical system. Humans appear to have evolved to deal with sharp environmental change in the form of climate fluctuations and their downstream effects (Boyd & Richerson, 1985; Ditlevsen, Svensmark, & Johnsen, 1996; GRIP, 1993; Potts, 1998; Richerson & Boyd, 2000). Given the coincident explosion in human brain size, it is likely that brain plasticity played a key functional role in supporting this kind of ecological resilience (Fiddes et al., 2018; Suzuki et al., 2018). The basic mechanisms of neuroplasticity originate deep in our vertebrate phylogeny (Finlay, 2007; Kirschner & Gerhart, 2005), but the fact that this metabolically expensive organ (Aiello & Wheeler, 1995b) expanded at such a rapid rate suggests that we have exploited these variation-harnessing mechanisms in unusually effective ways. The capacity for cultural variation and for brain plasticity created a doubly flexible system that deals rapidly and effectively with environmental variation.

Culture as a rapidly evolvable neurodevelopmental regulator

Brain plasticity is usually discussed in the context of reorganization of nervous systems in response to factors like somatic or neurological insult, sensory deficits, socio-economic deprivation, or training (Kolb & Gibb, 2014), and such conditions are commonly cast as deviations from normal input. Imagine if we were to talk about culture in the same way—as a system that enables populations to 'compensate' for non-normative environmental conditions. This view would hinge upon an illusory reference point; an unhelpful way to think about organization of culture. To fully appreciate the power of culture, instead of looking for variation around a fixed normative state, we consider the variation that culture enables: for example, the wide range of possible environments that individuals in a society are able to inhabit due to cultural knowledge—we spanned the globe as hunter-gatherers well before the advent of physics, chemistry or modern medicine. The same holds true for human brains—we should consider the space of possible phenotypes within the constraints of developmental rules. The brain is an adaptive organ not just in the sense of having a good functional fit with a particular environment; more fundamentally, it is adaptive because it is able to support *evolvability*—the ability of a population to respond effectively to environmental change by shifting its phenotypic distribution (Pigliucci, 2008; Wagner & Altenberg, 1996). In other species this is achieved by genomic change and levers around mutation rates. But humans, owing to cumulative culture, are able to adapt in the absence of genotypic change and at a much faster rate (Boyd & Richerson, 1985)—a principle that lies at the heart of cultural evolutionary theory. Most species who encountered the range of environments we live in would require considerable genetic change, but we achieved it with very little. For humans, the generation of neural variation and the generation of cultural variation are coupled processes.

Even in the absence of cumulative culture, human brains could still respond effectively to environmental change through standard learning mechanisms: there is evidence across mammalian and avian taxa that brain size explains the ability of species to adapt to new environments (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Bacher, Reader, & Lefebvre, 2008). In these animals, improvements in brain phenotypes are predominantly driven by either genetic adaptation or through direct interaction with the environment. But cumulative culture can, through its own evolutionary dynamics, incrementally improve or sophisticate the neural phenotypes that it produces even while there is no change in the environmental parameters to which the phenotypes are adapted, and at a much faster rate than genetic change. That is, the cultural environment is part of the environment for adaptation. Culturally induced brain phenotypes may exhibit an adaptive match with the non-cultural environment, but this is not because of direct exposure of the learning machinery of the brain to that environment—culture is able to vicariously take the place of environmental stimuli in shaping the nervous system toward a functional match.

For example, there may be some optimal level of risk-seeking in any given environment, which could be tracked either through variation in genes (e.g., neuromodulator genes for serotonin or dopamine; Kuhnen & Chiao, 2009; Kuhnen, Samanez-Larkin, & Knutson, 2013; Riba, Krämer, Heldmann, Richter, & Münte, 2008) or variation in experience (e.g., childhood adversity; Hellemans, Nobrega, & Olmstead, 2005; Lovallo, 2013). In non-cultural species, generation of the latter is dependent upon environmental affordances, and so a shift in the range of experiential variation can come about only through a change in the environment. But cumulative culture, through various channels spanning material artifacts, ritualized action, beliefs, and social norms, is able to furnish a much richer range of possible experience, some of which will be relevant to the programming of the degree of risk-seeking. This diversification would be useful in allowing a population to keep up with environmental change, but it would also be useful for pushing human neurodevelopment into particular regions of phenotypic space that could not be reached by non-cultural environmental input alone. Culture thus confers human populations with enormous flexibility in moving through the space of possible brain phenotypes. We can also expect that the cause-effect relationship between cultural practices and resulting phenotype will often be cryptic: not all cultural practices that influence risk-seeking will be overtly *about* risk, and there are likely to be many indirect, downstream effects of culture that impact neurodevelopment in non-intuitive ways.

These ideas about the role of phenotypic variability and evolvability have been a basic feature of cultural evolutionary theory since its inception (Boyd & Richerson, 1985), but the discussion has usually been described in terms of the transmission of particular, anthropologically salient skills in domains such as hunting and tool-making. Although the mathematical models are in no way restricted to such examples, the questions asked by researchers in the field have perhaps been unintentionally constrained by this discourse and its origins in anthropology. Here we suggest an extended focus of cultural evolutionary logic from observable behaviors to the organization of the brain.

All aspects of neuroplasticity are raw material on which cultural evolution can potentially act. Given that culture can design specific input regimes for the brain during its development, it has much more flexibility and control in programming the brain than genes do. We can thus expect significant interactions between the structure of neuroplasticity and the particular forms that culture adopts. There is insightful work suggesting for example that the shape of written symbols (Changizi et al., 2006; Changizi & Shimojo, 2005; Vinckier et al., 2007), the structure of speech (Giraud & Poeppel, 2012) as well as every other level of language organization (Christiansen & Chater, 2016b; Isbilen & Christiansen, 2018), and even the visual statistics of paintings both realist and abstract (Graham & Field, 2007) are all adapted to the intrinsic processing constraints of the nervous system. We believe however that the interaction between the learning gadgetry of the brain and cultural forms is likely to be much more varied and much more extensive. To uncover this mutual feedback, we will need to examine variation in cultural products as well as variation in cultural brains.

The focus on WEIRD populations has been a pragmatic choice that has brought us a wealth of preliminary knowledge about the human brain as expressed in one particular (and possibly peculiar) cultural context, but if we want to make sense of human brain function at a more fundamental level, we will need to study the brain across the range of extant cultural variability. This in itself does not give us a dynamic picture of neurophenotypic change in response to cultural evolution, but just as evolutionary biology has made great strides in inferring historical evolutionary trajectories based on the study of extant species, cultural neuroscience (Chiao, 2009; Kitayama & Uskul, 2011) gives us the material we need in order to interpret contemporary brains within a dynamic, cultural evolutionary framework. Cultural neuroscience is an area of research that looks at cross-cultural differences in neural response. But cultural neuroscience should not just be an additional level of subtlety that serves as a footnote to a “normal” WEIRD neuroscience—to the contrary, the cultural variation is the baseline that needs to be laid down if we are to pursue a science of the human brain that is faithful to its evolutionary history and basic adaptive utility. In the rest of this chapter, we will describe the framework of cultural evolution in more detail, and discuss how its insights necessitate a conceptual shift in the way in which we view the nature of brain development and the human mind.

The cultural evolutionary framework

Cultural transmission as evolutionary inheritance

Let's consider an ability almost synonymous with ecological competence in *Homo sapiens*: control of fire. Darwin (1871) believed that our ancestors' discovery of this skill was, "the greatest ever made by man, excepting language." There is evidence that the ability to use fire played a significant role in human evolution; in particular, fire allowed for the cooking of food and the cooking of food facilitated digestion and thereby contributed to the reallocation of tissue from the gut to the brain, both of which are metabolically costly organs (Aiello & Wheeler, 1995b; Navarrete et al., 2011; Wrangham & Carmody, 2010a). The control of fire is not a behavior that is typically learned by pure trial-and-error. Nor is it a genetically encoded behavior. Instead, we learn how to start fires and maintain them by watching or being instructed by other people. It is therefore a problem in which the search through possible solutions is radically narrowed down by social information. This approach to problem-solving – *social learning* – exploits the redundancy that exists when multiple agents (both in present and past generations) engage with the same problem: information about the past experiences of other agents can be used as a surrogate for actual exploration through the problem-space. This is not unlike how much better students would do an exam if they could copy each other's answers.

Social learning has been a significant topic of investigation in both human psychology and animal behavior (Bandura, 1977; Heyes & Galef, 1996; Hoppitt & Laland, 2013; Miller & Dollard, 1945), but it is research conducted within the framework of cultural evolution that has contributed most significantly to our understanding of the deep historical relationship between human ecological success and social learning. Cultural evolution describes how adaptive behaviors can be transmitted down generations not only through genetic inheritance, but also through social learning, and how in humans, extensive use of this second line of inheritance—culture—explains much of our success as a species (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Henrich, 2016; Laland, 2018; Mesoudi, Whiten, Laland, 2006). Humans employ a rich variety of technologies and other socially acquired skills that are adapted to local ecologies spanning much of the globe. Although social learning has been documented across diverse groups of animals including mammals, birds, fish, reptiles, and insects (Galef & Laland, 2005; Hoppitt & Laland, 2013b; Laland & Janik, 2006; Leadbeater & Chittka, 2007; Wilkinson et al., 2010), none come close to humans in the complexity of the information that is transmitted. Humans are the only species with clear evidence of *cumulative culture*: the accumulation of beneficial modifications over the course of iterated social transmission of behaviors to the point where the current level of complexity would be impossible for any individual to recreate on their own (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Dean, Vale, Laland, Flynn, & Kendal, 2014; Tennie, Call, & Tomasello, 2009). Cumulative culture is what has enabled the gradual refinement of numerous tools, techniques, and protocols over the history of our species, as well as the consequent mastery of diverse environments.

We have known for over a half-century how the molecular properties of DNA enable it to function as a genetic code (Crick et al., 1961), but when Darwin initially formulated the theory of evolution by descent with modification, he didn't know about the information-bearing substrate that underlies genetic inheritance nor did he even know about the basic principles of genetic transmission that were being discovered contemporaneously by Mendel. These strands of knowledge would come together in the early 20th century, in what is now known as the Modern Synthesis in evolutionary biology, but the concept of evolution itself was formulated at a level of abstraction that is independent of these biochemical and algorithmic details.

The logic of evolution stripped of its specific manifestations relies on three ingredients: variation in traits, inheritance of these traits between generations, and differential success in the survival of these traits. These criteria sufficiently explained the ubiquity of organisms that are well-adapted to their environments, removing reliance on teleological design or foresight. Because of this substrate-independence, the concept of evolution is not intrinsically limited to genetic inheritance. In *The Descent of Man*, Darwin himself postulated that the scope of evolution could be extended to domains of cultural knowledge, in particular that of language, when he wrote about how "the survival or preservation of certain favored words in the struggle for existence is natural selection" (Darwin, 1871).

Despite this initial conceptualization, the study of genetic transmission had been the main driver of evolutionary research throughout much of the twentieth century. The Modern Synthesis itself had been constructed on what was virtually an exclusively genetic perspective, a reasonable strategy for the time. This established approach partitions the heritability of traits into a genetic and environmental component. But over the years, there has been a gradual accumulation of evidence demonstrating that to fully understand phenotypic change, we need to look at multiple lines of inheritance other than genes and remove the one-way arrow of genes adapting to environments. This includes culture, but also epigenetic modulation of gene expression (Jablonka & Raz, 2009; Richards, 2006), mother-to-offspring transfer of microbiomes during vaginal childbirth, which is reduced in Cesearean births (Dominguez-Bello et al., 2016; Ley et al., 2008; Ochman et al., 2010), and inheritance of local environments that are modified through behavior—for example earthworms creating a more moist and richer soil in which subsequent generations can more easily survive (Odling-Smee, Laland, & Feldman, 1996; Odling-Smee, Erwin, Palkovacs, Feldman, & Laland, 2013). The theoretical view on evolution that attempts to incorporate all of these inheritance systems under a unitary framework is sometimes known as the Extended Evolutionary Synthesis (Laland, 2017a; K. N. Laland et al., 2015b).

Mechanisms of high-fidelity cultural transmission

Genetic transmission relies on a discrete molecular code that carries the information required to regenerate a full organism. In species with sexual reproduction, the genetic information carried by two individuals with complementary reproductive roles are recombined, resulting in offspring whose traits are correlated with both parents. Although cultural transmission also achieves the cross-generational inheritance of behavioral traits, it uses mechanisms that are very different from genetic transmission. One popular way to think about cultural transmission is the copying of information from one brain to another: Richerson & Boyd (2005, p. 61), assert that "culture is (mostly) information stored in human brains, and gets transmitted from brain to brain by way of a variety of social learning processes." But compared to the transmission of genetic information, the brain-to-brain pathway seems riddled with sources of information loss, even in a world of books, videos, and connected computers.

Given the enormous complexity of the behaviors that characterize human culture, how do humans transmit behavioral phenotypes through such a noisy channel?

One way in which humans overcome the challenge is through adaptations for causally-ignorant social learning. Researchers debate about the degree to which these adaptations are innate or constructed over the course of development (Heyes, 2003), but are generally unified in their recognition that human social learning unfolds at a level of complexity that is unprecedented in the animal kingdom (Boyd, Richerson, & Henrich, 2011; Csibra & Gergely, 2011; Mesoudi, Whiten, Laland, 2006; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). In particular, humans are thought to be proficient imitators who can perform high-fidelity copying of actions. Human imitation, unlike in chimpanzees, often involves mimicking the specific form of an action, even when the action includes details that are causally irrelevant with respect to the intended effect (Gergely et al., 2002b; Horner & Whiten, 2005; Lyons et al., 2007a). Although this trait can result in the imitation of ineffective or even maladaptive actions, it also supports the learning of actions whose effects are not immediately obvious. And critically, it doesn't require the learner to know the difference—this gets sifted and filtered over time at a population level through selective learning.

In addition to these adaptations on the part of learners, there is ample evidence that humans are also exceptional in the degree to which they provide guided instruction for the acquisition of behaviors (e.g. slowed down demonstration or teaching), a practice that is itself adapted to the degree of cultural complexity (we see more and more formalized teaching as cultural complexity increases; Kline, 2015; Muthukrishna & Henrich, 2016a). So heavy reliance on both social learning and teaching, at least at high personal cost, appear to be exceptional in humans. Beyond these adaptations of the learning procedure itself, human social organization (Hill et al., 2011; Tomasello et al., 2012; Wilson, 2012b) and life history (Gurven et al., 2006b; Schniter et al., 2015a) also make significant contributions to preparing conditions that are conducive to sophisticated social learning.

Whereas genetic transmission in humans only occurs from parent to child (*vertical transmission*), cultural transmission occurs among individuals within the same generation (*horizontal transmission*), as well as from older non-parents such as teachers (*oblique transmission*) (Cavalli-Sforza & Feldman, 1981b). In the early years of life, there is a strong emphasis on vertical transmission of cultural knowledge, as parents are the source of much of the learning that occurs in this period. As development proceeds through childhood and into adolescence, the oblique and horizontal channels become increasingly important, as they offer a greater number and variety of cultural variants from which the learner can choose. Vertical transmission is slow and conservative as it is constrained to specific relationships as well as to the generational time scale and is insufficient for cumulative culture (Enquist et al., 2010a). Horizontal transmission is unconstrained and can therefore enable the rapid diffusion of knowledge within a population, whereas oblique transmission is expected to be somewhere between these two. Because of these divergent properties, the kinds of knowledge that are transferred down these pathways will also differ.

In the case of vertical transmission, the learner has no choice regarding the model to be learned from, but in horizontal and oblique transmission, the number of available models will scale in proportion to the size of the learner's social network. Although learners benefit from acquiring the most effective cultural variants, it is often difficult to properly evaluate the effectiveness of behaviors, as cause–effect relationships can be ambiguous for a number of reasons, such as long time scales over which effects become manifest or the presence of multiple confounding variables. Due to the ubiquity of this kind of causal opacity (Lyons et al., 2007a), learners must rely on various methods for the selection of models, which are collectively referred to as *social learning biases* or *social learning strategies* (Heyes & Pearce, 2015; Laland, 2004; Rendell et al., 2011). There are a large number of social learning strategies that have been proposed as having utility based on either empirical observation or theory (Kendal et al., 2018; Rendell et al., 2011). Two examples of strategies that are thought to be significant in the context of human culture are the *conformist bias* (Henrich & Boyd, 1998; Muthukrishna, Morgan, & Henrich, 2016), in which learners disproportionately tend to adopt behaviors that are observed frequently, and the *prestige bias* (Cheng et al., 2013; Chudek et al., 2012; Henrich & Gil-White, 2001a), in which the number of learners already attending to a model is taken to be a cue for the desirability of that model's behaviors. Both of these strategies are expected to be effective ways of selecting adaptive behaviors without having to explicitly evaluate their utility. But this of course involves a trade-off between efficiency and certainty, and sometimes these strategies can result in the propagation of sub-optimal or even maladaptive behaviors. One strength of the cultural evolutionary framework is how it can explain the spread of maladaptive behaviors through the lens of evolutionary dynamics.

These cultural evolutionary processes indicate how useful information can spread from brain to brain in an effective manner, but the descriptions fall short of being able to explain how brains become sophisticated enough to carry and transmit this kind of knowledge in the first place. Cultural evolution is only one part of the picture; in order to understand the role that culture plays in the evolution of organisms, we must, at minimum, understand brains and the coevolutionary dynamic between brains and culture.

The cultural brain hypothesis: How culture shaped our brains over evolutionary history

Just as genetic information is stored in the nucleotide sequences of genomes, cultural information is stored in the neuronal connections of brain tissue (at least until the advent of writing and other forms of distributed cognition). Brains can be scaled in capacity and complexity by evolution, with larger, more complex brains enabling more storage and more sophisticated processing, but with larger energy requirements (Aiello & Wheeler, 1995b; Henrich & Boyd, 2008; Kuzawa et al., 2014; Leonard et al., 2003). Humans are an extreme in both brains and energy usage. Our brains tripled in size over the last few million years and are three times as large as chimpanzees, our closest cousins (Bailey & Geary, 2009; Falk, 2012). We also use energy at a faster rate than any other great ape (Pontzer et al., 2016), an achievement we sustain thanks to our efficient extraction of energy from our environment. This efficiency is thanks to culturally acquired food processing techniques, such as cooking, cooperation in food acquisition, parental provisioning, etc., and more recently, the division of labor (Hrdy, 2011a; Kaplan et al., 2000b; Tomasello et al., 2012; Wrangham & Carmody, 2010b). Even our life histories are aligned with this interpersonal transfer of knowledge—we require an extended period of learning in order to acquire cultural knowledge, whether advanced hunting skills or modern classroom education (Gurven et al., 2006b; Koster et al., 2019; Schniter et al., 2015a; Schuppli et al., 2012), and indeed, this period may be further extending in developed societies today with longer periods of learning and delayed reproduction (Muthukrishna & Henrich, 2016b).

As we can see, there is a complex relationship between sociality, energetic budget, culturally transmitted knowledge, brain size, and life history. In the case of humans, these factors appear to have worked together synergistically, yielding distinct human phenotypes, but the ways in which these variables interact may reflect a more general set of principles that explains evolutionary trajectories across diverse animal taxa. This is the approach taken by the *Cultural Brain Hypothesis* (Fox, Muthukrishna, & Shultz, 2017; Muthukrishna, Doebeli, Chudek, & Henrich, 2018), which is grounded in theoretical insight from cultural evolutionary theory and empirical observations from the animal behavior literature.

A survey of the literature on primate and human brain evolution reveals a diverse array of explanations for the expansion of brain size that occurred multiple times in primate phylogeny. The most influential such theory over the last two decades has perhaps been the Social Brain Hypothesis (Dunbar, 1992; Dunbar & Shultz, 2007), which claims that primate brains expanded in order to be able to keep track of inter-individual relationships in increasingly large groups; this was later modified to include other aspects of social living. Theories that link primate brain size expansion to various kinds of ecological problem-solving have been influential as well (Barton, 1998; DeCasien et al., 2017). A third strand are explanations that attribute primate brain expansion to the ability to learn adaptive behaviors from conspecifics, i.e., social learning (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Reader, Hager, & Laland, 2011; Reader & Laland, 2002; Street, Navarrete, Reader, & Laland, 2017; van Schaik & Burkart, 2011; van Schaik, Isler, & Burkart, 2012). The CBH moves the focus from 'social' or 'ecological' to 'learning' more generally, but in doing so, also generalizes social and ecological theories.

The CBH formally models the specific causal structure that generates the covarying relationships among variables such as brain size, group size, reliance on social learning, the degree of adaptive knowledge available in the population, and life history profile (Figure 6.1); other theories linking brain evolution to social learning have tended to be more ambiguous about the causal relationships that underlie the covariation. This causal structure builds on other cultural evolutionary theory and is consistent with findings in the empirical literature. Because the CBH is based on a theoretically motivated, process-level model rather than being derived from observations of a particular subset of animal species, it is able to make predictions across the whole space of species traits. For example, it is able to describe how the strength of the relationships between the mentioned variables are expected to vary across the entire gamut of sociality, from the most solitary to the most gregarious species. For example, the CBH predicts that the correlation between brain size and group size should be significantly stronger in species that engage in social learning than in those that do not.

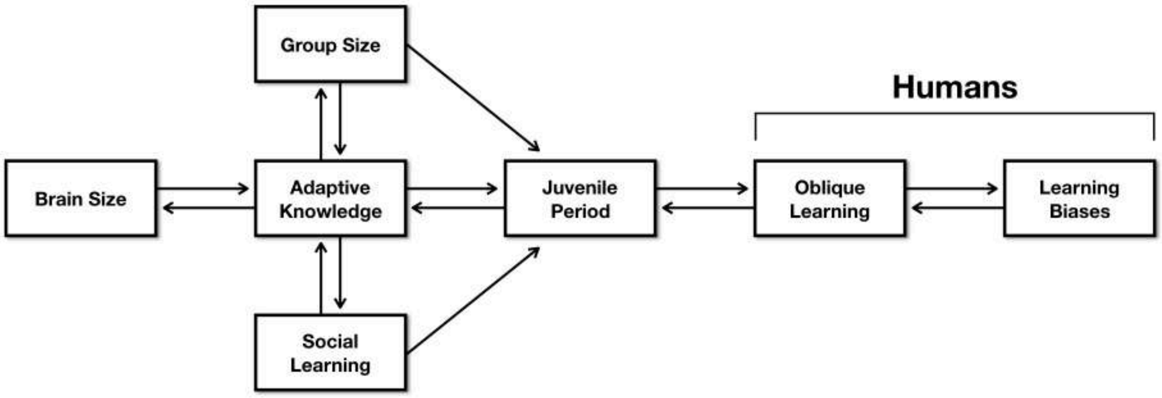

Figure 6.1: Causal relationships predicted by the Cultural Brain Hypothesis (adapted from Muthukrishna et al., 2018)

Relatedly, the model presents predictions for the human evolutionary trajectory, with its extreme reliance on cumulative culture, as a special case of the general causal process rather than as something requiring a unique explanation. These predictions are referred to as the Cumulative Cultural Brain Hypothesis (CCBH). In particular, the model predicts two attractors toward which species tend to converge over evolution: one that relies mostly on asocial learning (e.g., trial-and-error learning), but with some amount of social learning usually also taking place, and another that is dominated by social learning. The social learning regime has an extreme that evolves in conditions in which an autocatalytic takeoff occurs through positive feedback between brain size, adaptive knowledge, and sociality—the result being species in which the level of the adaptive knowledge acquired by individuals greatly exceeds the level that could plausibly be achieved through asocial learning alone. The model operationalizes cumulative cultural evolution (Dean et al., 2012; Dean et al., 2014; Tennie et al., 2009) based on a region where the probability of acquisition through asocial learning is exceedingly unlikely; a human regime.

The CBH gives us a conceptual handle on the kind of dynamics that can explain the covariation among traits such as brain size, length of juvenile period, sociality, and cultural complexity (i.e., level of adaptive knowledge), and does this by making explicit the underlying causal structure. Its explanatory power extends into the case of the human evolutionary trajectory, which exhibits a profound acceleration across all of these variables. However, although the model has many moving parts, its rendition of the brain is representationally minimal: an index of size. In the remainder of this chapter, we will attempt to link the evolutionary dynamics portrayed by the CBH to a more detailed examination of neural architecture and plasticity.

Large brains and their concomitants

Large brains and the degrees-of-freedom problem

We begin with the principle that as brains become larger, they offer more degrees of freedom in configurability. In mammalian evolution, increased brain size does not result in a linearly corresponding increase in the size of sensory organs—for example, species with vastly different brain sizes have relatively similar eye sizes (Howland et al., 2004). Larger brains do not take in a significantly increased amount of raw data—instead, they provide a greater range of ways in which the same data can be filtered, decomposed, and recombined. Big brains allow more processing and storage options. Roughly the same can be said for action: the difference in brain size between a human and a chimpanzee (a factor of ~3) far outstrips the difference in body size or musculoskeletal organization, but the larger human brain allows for a much wider breadth of options for decision-making and behaviour, including various forms of behavioural inhibition (Damasio, 1994; MacLean et al., 2014).

We can therefore say that larger brains enable enhanced control over both sensory processing and action selection, although in actual brain function these two things are deeply intertwined and neither anatomically nor functionally separable (Cisek & Kalaska, 2010; Varela et al., 1991). So large brains not only amplify control options in the sensory and motor domains respectively, but also in coordination. In the field of cognitive neuroscience, this latter mediational function is referred to as *cognitive control*. The term is roughly synonymous with the older term 'executive function', and Botvinick, Carter, Braver, Barch, & Cohen, (2001) describe it as "the ability [of a cognitive system] to configure itself for the performance of specific tasks through appropriate adjustments in perceptual selection, response biasing, and the on-line maintenance of contextual information." Cognitive control is a higher-order concept that subsumes component functions such as attention, working memory, error monitoring, inhibitory control, and planning. Cognitive control usually refers to the ability to modulate brain function in real-time and in a task-dependent manner, but this kind of adaptive configuration of brain function can also be achieved in part by constraints that stem from processes unfolding over longer time scales, such as brain development and, as we argue, cultural evolution (or more specifically, brain–culture coevolution). The general problem of proliferating control options in large brains demands solutions that span such time scales.

There are at least three characteristics of large brains that make this job easier: One is hierarchy—a hierarchical cortical architecture is able to organize its representations in a combinatorially efficient manner, and owing to fundamental neurodevelopmental constraints, the depth of the cortical processing hierarchy scales systematically with brain size (Charvet, Cahalane, & Finlay, 2015; Finlay & Uchiyama, 2015). This is the same computational principle that explains why artificial neural networks become substantially more powerful simply by increasing the number of layers (LeCun et al., 2015). Another characteristic of large brains is the protracted developmental duration that is required to grow them. Brain growth follows a fixed trajectory that is more or less species invariant (Passingham, 1985), and for larger brains, this developmental structure supplies a longer absolute window over which mechanisms of early-life plasticity can be exposed to input from the world. Larger brains therefore undergo more shaping by extrinsic stimuli, or in other words, can learn more. Across all species, this shaping will align with the structure of the ecological environment, but a species with cumulative culture is able to impose additional regimes of shaping that do not exist in the environment per se. Finally, because brain tissue is metabolically expensive, large brains also require greater nutritional provisioning, such as from a calorie-rich environment, availability of food acquisition techniques to be learned or early provisioning from parents or alloparents.

This relationship between large brains and sociality is conducive to the acquisition of adaptive forms of functional configuration via social learning (see Muthukrishna et al. (2018) for a discussion of the two pathways to larger brains).

Brain expansion brings with it a surfeit of processing options, but because it is also accompanied by useful properties like the three properties above, there is greater opportunity for converging on adaptive processing options. Culture can play a significant role in this search process, as it is able to change at a much more rapid rate than either genes or the ecological environment. It is also able to support variation in input that would not exist otherwise, which in turn increases phenotypic variability and hence evolvability. Let us examine each of the mentioned concomitants of large brain size in more detail.

Concomitant 1: Large brains and deep hierarchical abstraction

Larger brains don't just enable an increase in the amount of stored knowledge; they also allow for new ways of representing knowledge. As the neocortex grows larger over evolutionary time, the sizes of early sensory and motor areas expand relatively slowly compared to transmodal association areas that are uncommitted to any particular sensory modality. The largest brains are thus the ones with the greatest proportion of association cortex (Krubitzer, 2009). More association cortex means deeper representational hierarchies, and thus the encoding of increasingly abstract kinds of information, such as complex, context-dependent rules for action, or a holistic and variation-tolerant grasp of objects instead of just simple sensory snapshots (DiCarlo et al., 2012). Deeper representational hierarchies also support greater cross-modal integration, so that signals from different sensory systems can be bound together into abstract representations that are independent of particular modalities. For example, speech acquisition in human infants requires the learning of cross-modal associations between visual, auditory, and motor signals.

Human neuroimaging has shown that lateral frontal cortex and parietal cortex—both patches of association cortex—are organized in a functional hierarchy of the kind described above, with increasing levels of cognitive abstraction being arranged roughly along a caudalto-rostral axis (Choi, Drayna, & Badre, 2018). Increasingly complex tasks (e.g., nesting of conditional rules) recruit cortical areas that correspond to higher levels of the processing hierarchy. Across individuals, a measure of hierarchal organization as estimated by Dynamic Causal Modeling (Friston et al., 2003) not only predicts performance in an explicitly hierarchical cognitive task, but also demonstrates a sizable correlation (r = 0.61) with a composite intelligence measure that comprises working memory and fluid intelligence (Nee & D'Esposito, 2016). Degree of hierarchical organization may well be an important mediator of the relationship between brain size and intelligence within humans (Gignac & Bates, 2017), as well as across species (MacLean et al., 2014).

In perception too, hierarchical organization is what enables complex forms of object recognition. Deeper levels of the processing hierarchy support abstract representations that are increasingly tolerant to any number of dimensions of variability such as angle of view, within-category variation of exemplars, or sensory modality (DiCarlo et al., 2012). The human visual system is literally able to abstract out the essential features of some target of interest, as illustrated vividly by the discovery of 'Jennifer Aniston neurons'—single cells in the medial temporal lobe that respond to a specific individual across various photographic and hand-drawn renditions and even to their printed name, but not to representations of any other individuals (Quiroga et al., 2005). This is precisely the sort of abstraction that is characteristic of a concept or a semantic representation, and in fact it is commonly thought that the anterior temporal lobe, an association area that corresponds to the deepest stage of the ventral visual stream, functions as a hub for the representation of semantic meaning (Chadwick et al., 2016; Patterson et al., 2007).

In general, the more topologically distant a given cortical area is from the primary sensorimotor areas, the more abstract its domain of representation will be. The default-mode network (Raichle, 2015) coincides with the cortical areas that are furthest in this respect (Huntenburg et al., 2018), and not only do these deep association areas display the highest level of cross-modal integration, they also encode the longest temporal windows (e.g., sentences vs. phonemes; Hasson, Chen, & Honey, 2015) as well as the most abstract semantic concepts (e.g., 'schools' and 'lethal' vs. 'yellow' and 'four'; Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016). In terms of function, this set of areas is known to be most active when dealing with processes such as mind-wandering, mental time-travel (i.e., episodic recollection and thinking about the future), autobiographical memory, narrative comprehension, and social cognition (Spreng et al., 2009). These functions are therefore expected to be the ones that require the most hierarchical depth and hence brain size.

The fact that social cognition, in particular the family of cognitive functions known as "theory of mind", is firmly tied to the network of cortical areas that are at the leading edge of brain expansion is interesting (Schilbach et al., 2008), as it suggests that large brains are not only useful for the social learning of advanced skills, but also for understanding the social domain itself. Areas recruited during visual processing of conspecific interactions appear to occupy similar cortical regions (Sliwa & Freiwald, 2017). The fact that these areas encode temporal depth is also significant, as a sophisticated understanding of the behaviour of others requires that they be situated within an extended situational context, such as social scripts (e.g., the event structure of 'birthday party'; Krueger, Barbey, & Grafman, 2009) or narratives (Nguyen et al., 2019; Simony et al., 2016; Zacks et al., 2010). In large-brained species, the behaviour of conspecifics is a source of some of the most complex information in the environment (Humphrey, 1976), and it makes sense that the neural representation of the social world will be accommodated by cortical areas that are at the deepest levels of the processing hierarchy. Brain expansion enables a richer representation of the social world.

Concomitant 2: Large brains and longer development

The relationship between brain size and the length of neurodevelopment is highly systematic. For example, the Translating Time model of Finlay and colleagues (Finlay & Uchiyama, 2017; Workman et al., 2013) is able to use a highly parsimonious but neurodevelopmentally realistic model to predict the nonlinear trajectory of whole brain growth across a variety of mammalian species, along with hundreds of other neurodevelopmental events that span the gamut from the appearance of specific axonal connections to the emergence of walking. For brain growth, the correlation between predicted timing and observed timing is on the order of $r = 0.99$, demonstrating just how systematic brain growth is even when comparing across phylogenetically distant species whose brain masses differ by a factor of ~1000, such as a human vs a mouse (Halley, 2017; Passingham, 1985; Workman et al., 2013a). The idea underlying this research is that evolution can create larger brains by temporally stretching the highly structured process of brain development that has been conserved since the ancestor to all extant mammals.

If we look at specific durations, the mouse for example reaches 50% of adult brain mass around 26 days post-conception or 7 days postpartum (A. Gottlieb et al., 1977), while humans reach the same milestone around 350 days post-conception or 2.5 months after birth (Dekaban & Sadowsky, 1978). We are using 50% brain mass as an arbitrary reference point, but any such reference point can be highly informative precisely because of the systematic and predictable nature of mammalian brain development: if we know the timing of some particular developmental event, we know with a significant degree of accuracy the developmental state of the nervous system as a whole. When the mouse is at its 50% mark, everything else going on in its cranium—the onset and offset of neurogenesis in particular cortical layers, the establishment of dopaminergic axons from the midbrain to the neocortex, or the completion of myelination in the hippocampus—is at roughly the same state as it is in the brain of a human infant who is also achieving the 50% milestone (Workman et al., 2013a).

Now consider the interval between 50% and 80% adult brain mass: the mouse progresses through this segment of the neurodevelopmental process (along with every other event that is in sync with it) in a span of just 5 days (Gottlieb et al., 1977), while the human takes about 16 months to go through it (Dekaban & Sadowsky, 1978). The two species are undergoing roughly the same degree of intrinsic brain development within this interval, but for the human infant, the processes of brain development are exposed to more than a year of external stimuli, while the baby mouse only gets a few days. Although it is true that the time scale of an organism's physiological and ontogenetic processes scale down systematically with body size (West et al., 2001), there is simply no way to close the gap in the amount of learning that can occur between the mouse and the human, both within this particular interval and across brain development as a whole. So increasing brain size does not only increase processing power, it also allows more knowledge and skills to be loaded into it during its development, whether this be through trial-and-error or social learning.

In fact, there is likely more to the story than just a longer window of opportunity for learning. The brain itself is of course undergoing considerable organizational changes over development, and this appears to create a learning gradient that unfolds over time, in which early learning is characterized by a broader space of hypotheses about the structure of the world and hence greater flexibility in learning. As maturation progresses, the brain acquires stronger prior hypotheses about what to expect, and information processing becomes more efficient, but also more rigid, consistent with evidence from learning (Gopnik et al., 2017; Lucas et al., 2014).

Making a similar proposal, but with greater neurodevelopmental specificity, Chrysikou and colleagues (Chrysikou, Weber, & Thompson-Schill, 2014; Thompson-Schill, Ramscar, & Chrysikou, 2009) hypothesize that the extended development of the prefrontal cortex and the resulting deficiency of prefrontal function in children (Diamond, 2013) is not a deficit per se, but rather a functional design feature that affords certain learning advantages that are critical in early years. For instance, in language acquisition, children are better at learning irregular verbs and irregular plurals than adults are, and this is attributed to the tendency for children to reiterate utterances that they have actually heard, compared to adults, who tend to search for underlying rules (Boyd & Goldberg, 2012). This tendency would give children an advantage in learning conventions in general, linguistic or otherwise, because in this domain, veridical reproduction (overimitation) often matters more than finding efficient representations (Lyons et al., 2007b).

Reduced prefrontal control early in life may thus confer an advantage in the effective execution of conformity. Paradoxically, it may also confer an advantage for innovation as well (Chrysikou et al., 2014). Older children are more susceptible to 'functional fixedness' effects than are younger children, meaning that once they have a concept of what a given tool is for, they have more difficulty coming up with alternative uses for it (Defeyter & German, 2003). There appears to be a marked shift in this tendency between the ages of 5 to 7 years, a period during which prefrontal development is beginning to accelerate (Kanemura et al., 2003). There is also evidence that links prefrontal activity to inhibited performance when adults are asked to come up with novel uses for tools (Chrysikou et al., 2013; Chrysikou & Thompson-Schill, 2011). More generally, artistic creativity may be tied to a reduction of prefrontal control, whether in visual art or jazz improvisation (Chrysikou et al., 2014). These advantages of reduced prefrontal function or *hypofrontality* necessarily accompany the early phase of brain development in a species like ours, in which the mammalian neurodevelopmental program is lengthened to generate a large brain. In other words, large brains, which in the case of humans are also cultural brains, get these advantages 'for free' in evolutionary terms—specific selection is not required. And it is not difficult to see why a mutually beneficial relationship between cultural learning and early hypofrontality is plausible. These findings are important to building a more complete picture of human evolution. They inform our understanding of the raw material that natural selection can work with, mapping out the adjacent possible and guiding us in inferring necessary selection pressures and probable adaptations. And although they echo similar dynamics between variation creation and transmission fidelity at a population level (Muthukrishna & Henrich, 2016b), at an individual level, they are thus far missing from dual inheritance theory and cultural evolution.

Concomitant 3: Large brains and sociality

Brain tissue is expensive and a large, complex brain needs to pay its energy bills. For humans, at least in early life, provisioning comes from nutritional subsidies offered well beyond nursing and often beyond mothers and even close kin (Hrdy, 2011a). Such provisioning requires stable nutritional surpluses, made possible by effective methods for calorie acquisition from cumulative cultural knowledge. The transfer of food resources from the competent to the incompetent appears to be a human universal, and individuals may not attain a production surplus until late into their teens or beyond, meaning that humans go through a long period of dependence during which they acquire the skills needed to produce at a surplus for the next generation (Kaplan et al., 2000b). In contrast, chimpanzee juveniles are forced to look after themselves immediately after weaning.

When we evaluate the timing of weaning in relation to the stage of brain maturation across species, we discover that human infants are actually weaned at a noticeably earlier point in the mammalian neurodevelopmental schedule than our closest primate relatives (Finlay & Uchiyama, 2017; Hawkes & Finlay, 2018), and this is also reflected in the timing of weaning being earlier than expected on the basis of brain size: Figure 6.2 (weaning) shows that human weaning occurs much earlier than would expected for a non-human ape with our brain size, and earlier even than would be expected for other primates (i.e., monkeys and prosimians). The box plot displays the range in the timing of weaning across small-scale societies as observed in ethnographic records (Sellen, 2001), revealing substantial variation in human weaning: half of these societies lie below the lower boundary of the 95% prediction interval for apes, and about 1 out of 6 lie below the lower boundary for other primates. These data suggest that in humans, the timing of weaning is determined by both genetic and cultural selection.

Early weaning is tied to a shorter period between births, and hence higher reproductive output. It is striking that the hunter-gatherer inter-birth interval of 3 to 4 years is shorter than the 4 to 5 year interval of chimpanzees and gorillas (Robson & Wood, 2008) despite humans being more delayed than the great apes in other aspects of life history, and this is even more remarkable once we take the relationship between brain size and life history into account. Early weaning is possible thanks to care given by not just mothers but also others (Hrdy, 2011a). This high level of sociality also ensures access to a broad assortment of conspecifics at an early stage of life, which may have helped in the evolution of selective social learning biases that extend cultural learning beyond parents and close kin (Muthukrishna, Doebeli, et al., 2018a; Muthukrishna & Henrich, 2016a). The energetic demands of our large brains may thus link us not only to social structures that are able to supply the requisite calories, but also to cultural networks that transfer adaptive information as well.

Another exceptional feature of human life history is our long lifespans (Figure 6.2 reproductive lifespan and maximum longevity). The puzzle of human longevity, including the postmenopausal years, has been a topic of much discussion in the anthropological literature (Hawkes, 2003; Kaplan et al., 2000a), but here we suggest that this feature too may be partly explained by genes adapting to the requirements of cultural learning. In particular, an ever-expanding corpus of skills and knowledge may select for longer lifespans over which more of this cultural knowledge can be acquired and refined and a longer period for it to be exploited or passed on to the next generation (Information Grandmother Hypothesis). Even in relatively simple societies that rely on hunting and 'slash-and-burn' agriculture, competence in foraging skill can peak as late as the 50s (Gurven et al., 2006a; Schniter et al., 2015b), and this may just be a manifestation of a more general positive relationship between social complexity and the late peaking of foraging skill that is observed across mammalian species (Isler & van Schaik, 2009). Accumulation of knowledge may also explain postmenopausal life in other highly social species such as killer whales (Brent et al., 2015). In contrast to traits such as weaning and lifespan, birth and sexual maturity appear to occur in humans at roughly the timing that would be expected for both apes and non-apes (Figure 6.2 gestation and sexual maturity), suggesting differential selection pressures across different facets of life history.

We have reviewed three traits that covary positively with brain size: deep hierarchies, long development, and high sociality. When brains expand over evolution, this suite of traits gets pulled upward, in some parts as expected, and in other parts deviating from expectations and therefore probably requiring trait specific genetic, cultural, or culture-gene coevolutionary selection. A cultural evolutionary neuroscientific approach thus informs cultural evolution and informs neuroscience.

When cultural knowledge, brain size, and access to the number of brains (i.e., population size) enter a positive feedback loop, as predicted by the Cumulative Cultural Brain Hypothesis (Muthukrishna, Doebeli, et al., 2018a) these concomitants of brain expansion play a role in moving information processing from simply the cranial-bound brain to the collective brains bound in a social network, which can in turn empower each individual brain via cultural learning (Muthukrishna & Henrich, 2016b).

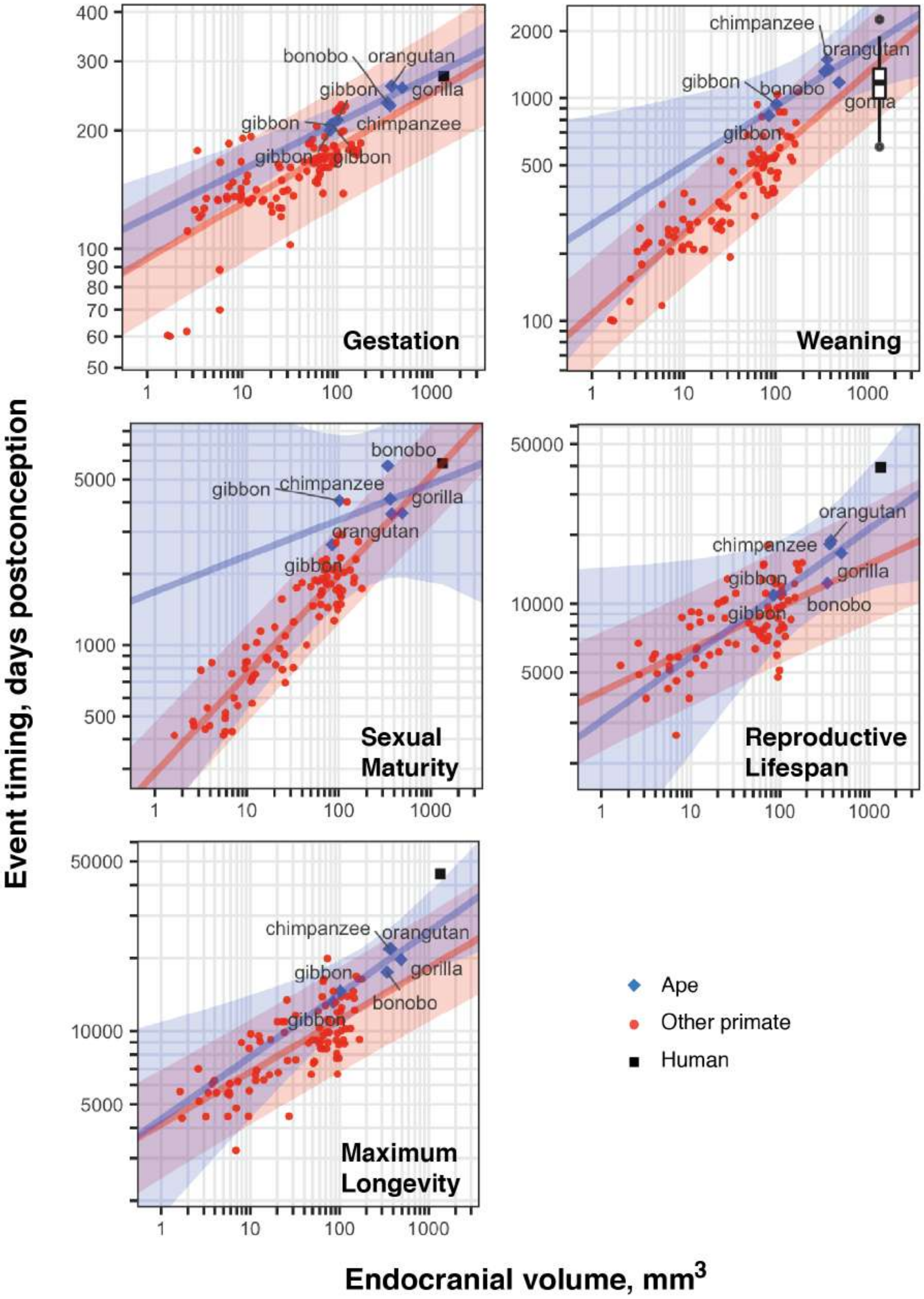

Figure 6.2: Scatterplots displaying the relationships between brain size (endocranial volume) and timing of life history events among primates, for gestation, weaning, sexual maturity, reproductive lifespan, and maximum longevity. Event timings are given in postconception days rather than postnatal days because the former is tightly coupled with the species-invariant state of brain maturation, whereas the latter is not (Workman et al, 2013). Blue

and red lines are OLS regression lines for non-human apes and other primates (i.e., monkeys and prosimians), respectively. Lightly colored bands are regions within the 95% prediction intervals for each model. Humans are plotted, but not included in the computation of the models. The box plot in the panel for human weaning displays the range in the timing of weaning across the ethnographic record, based on Sellen (2001). All plotted data are from Street, Navarrete, Reader & Laland (2017) except for the human endocranial volume of 1349 cm^3, which is the average value across 122 ethnic groups from Beals, Smith and Dodd (1984), and for the distribution of human weaning.

Cumulative culture and the rise of the collective brain

Humans are thought to be the only species for which we have evidence of cumulative culture (Dean et al., 2012; Dean et al., 2014; Tennie et al., 2009), and the Cultural Brain Hypothesis (Muthukrishna et al., 2018) models this evolutionary trajectory as the crossing of a threshold in which the individuals that make up a species begin to learn more adaptive knowledge from social learning than they would be able to discover by themselves: Cumulative Cultural Brain Hypothesis. Once this threshold has been crossed, traits like sociality, brain size, length of juvenile period, and cultural complexity enter a positive feedback loop and shoot upward rapidly. Note that in a scenario like this one (which captures various anomalies of human evolution), large brains can be maintained only because they can come into the world with the expectation that they will be fed with energy and information that is effective enough to be able to pay for their high metabolic cost. In such a species, groups grow in such a way that their collective information processing capacity eclipses the intrinsic capabilities of the neural hardware itself, and individual brains become informationally and metabolically dependent on others in their societies. The processing power of the group is determined by factors such as the number of individuals that constitute them, by the topology of connections between individuals, and by the effectiveness of strategies for selecting what to learn and who to learn from (Derex et al., 2013; Derex & Boyd, 2016; Goldstone & Theiner, 2017; Henrich, 2004a; Muthukrishna et al., 2013; Muthukrishna & Henrich, 2016b). But inference of the adaptive value of any given behavior or belief is inherently noisy and opaque, as we saw in the discussion on social learning strategies, and so there is always a selection pressure for better search strategies. Former CEO of Google Eric Schmidt unknowingly echoed these insights about the coevolutionary dynamics of culture in 1993 when he quite presciently predicted that, "when the network runs as fast as the computer backplane, the computer will hollow out and distribute itself around the network, and profits in the industry will migrate toward the providers of 'sort' and 'search' capabilities." (Gilder, 2013, p. 319). We can say that Schmidt's vision concisely captures what has been happening to the relationship between computer hardware, software, and networks in recent years. So too in brains, culture, and sociality.

The evolution of human brain *size* is well-known even among non-scientists, and discussions of brain evolution often revolve around this manifestly visible characteristic. But according to the perspective that we are outlining here, a focus on size, or for that matter any property of individual brains, is insufficient for explaining human brain evolution. Our social systems, our bodies of culturally accumulated knowledge, our social learning strategies, and even our life histories have all evolved together with our brains, and we need to think of all these factors as an integrated system. To not do so is as misguided as trying to understand the advances in computing solely through understanding advances in hardware specifications.

Muthukrishna and Henrich (2016) refer to this distributed information-processing system as a *collective brain*, nomenclature that emphasizes the information-processing capacities of the network itself. They argue that collective brains are underpinned in particular by our *norm psychology* (Chudek & Henrich, 2011) and *ethnic psychology* (McElreath et al., 2003). Norm psychology refers to the suite of abilities that allow us to infer what the shared behavioral standards of the group are, adhere to them appropriately, and enforce them when flouted. Ethnic psychology refers to the mental abilities that allow us to figure out to which groups we belong. In combination, our norm and ethnic psychology allow us to understand the norms of these groups and to whom these norms apply. Once we have a norm psychology and an ethnic psychology, societies are able to generate complex structures in their networks, for example through marriage rules that have consequences for the shape of networks beyond immediate kin (e.g., through in-law relationships) and thus for the parameters of the collective brain. Societies also vary on how open they are to out-group members (e.g., whether exogamous marriage is allowed or to whom; Chapais, 2013; Hill et al., 2011), how tolerant they are to norm deviations (e.g., tightness-looseness; Gelfand et al., 2011), and their amount of migration (Powell et al., 2009). Each of these traits, and no doubt many more, modulate information flow in the collective brain. And since these collective brains in turn change their constituent cultural brains, we complete the circle and find ourselves needing not just a neuroscience approach, but a cultural neuroscience approach to cultural evolution and a cultural evolutionary approach to cultural neuroscience.

Much of cultural neuroscience has focused on mapping cross-cultural differences at level of the brain (just as cultural psychology has mainly focused on mapping cross-cultural differences in psychology). A more systematic approach to cultural evolutionary neuroscience requires an understanding of the sources of those cross-cultural differences (e.g., Schulz, Bahrami-Rad, Beauchamp, & Henrich, 2018) and how they manifest neurologically as well as perhaps genetically, such as via a Baldwinian process (Crispo, 2016) where repeated cultural learning eventually selects for genes that make that learning more effective or more efficient.

Caveats and Conclusions

Cultural neuroscience has revealed variations in human brains, particularly between East Asians and Western people, who appear to differ even in core aspects of psychology, such as visuo-spatial judgment (Goh et al., 2013), arithmetic (Tang et al., 2006), and empathy (Cheon et al., 2011). But variations in the neural systems underlying common tasks are present even within a population, because our brains are as variable as we are. For example, Noppeney and colleagues (Noppeney, Penny, et al., 2006; Noppeney, Price, et al., 2006) examined intersubject variability in fMRI activity while participants underwent semantic judgment tasks, within a conventional UK participant sample. Such variability is usually discarded when data is averaged across participants, but Noppeney et al. used analyses that allow detection of differences in the neural systems being recruited for the same task. Across two different experiments, they found overlapping but distinguishable clusters of participants, with each participant-cluster corresponding to a different activation profile and suggesting the use of a distinct strategy—for example, semantic discrimination being supported by stimulus-dependent ('bottom-up') versus task-dependent ('top-down') mechanisms (Noppeney, Price, et al., 2006). In this case these differences in neural activation did not predict differences in performance.

The general notion that multiple neural systems can interchangeably implement a common function is an example of what is known as *degeneracy*, defined by Edelman & Gally (2001) as "the ability of elements that are structurally different to perform the same function or yield the same output", or in other words, a many-to-one structure–function mapping

(Edelman & Gally, 2001; Price & Friston, 2002; Tononi et al., 1999). The extent of degeneracy in the genetic code is striking: In *C. elegans*, 89% of single-copy (i.e., non-duplicated) genes can be knocked-down without any detectable phenotypic effect (Conant & Wagner, 2004). Across levels of biological organization from genes to multiply realizable muscular control of movement, degeneracy is taken to be a key factor in supporting robustness and evolvability, as it enables the generation of phenotypic variation without any immediate consequence for adaptive function and thereby supports the exploration of phenotypic space (Ancel & Fontana, 2000; G. M. Edelman & Gally, 2001; Whitacre & Bender, 2010). Although the extent of degeneracy in the brain is not currently known, it has been argued that the rapid recovery of function following focal cortical damage is possible only because neural degeneracy is prevalent (Noppeney et al., 2004). Thus caution is required when we find cross-cultural differences in neural activity, as they may not necessarily correspond to differences in function. Gordon et al. (2015) found individual differences in the topology of resting state functional connectivity but warn that such whole-brain architectural differences may not necessarily be predictive of cognitive performance and may instead reflect degeneracy. Cultural psychologists have illuminated an impressive collection of cross-cultural psychological differences, but the general strategy of mapping these performance differences onto neural activation differences requires caution, and we should be wary of false positives. In principle, explanations for such behavior–brain mapping are constrained by cultural psychological constructs, such as when greater activation of theory of mind-related areas of the brain in East Asians is attributed to their 'collectivism' (Han & Ma, 2014), but there is ambiguity in the specific predictions that can be derived from such constructs, and their effectiveness as theoretical constraints for making sense of high-dimensional neuroimaging data is not self-evident.

There are also cases in which an apparent absence of performance difference masks some interesting underlying neurocognitive differences. Comparing patients with Williams Syndrome, a developmental disorder characterized by intellectual impairment in some domains but intact ability in others, with healthy controls, Karmiloff-Smith and colleagues found that the two groups achieve matched performance on some tasks using different cognitive strategies. For example, children with the disorder rely comparatively more on verbal abilities than on visuo-spatial abilities when counting (Ansari et al., 2003), and adult patients were found to use 'featural' as opposed to 'configural' processing in face perception tasks (Karmiloff-Smith et al., 2004). Although the example is of a clinical population, studies such as these hint at what we should also be looking for cross-culturally, namely, covert variation in neurodevelopmental trajectories.

In other cases, cross-cultural and within-population differences in neural activation do affect overt performance, such as in the neural response to threat (Coan et al., 2006, 2017), or is likely to have performance implications, such as the relationship between age and brain structure (LeWinn et al., 2017), reading and writing (Bolger et al., 2005a; Kobayashi et al., 2007; Tan, Laird, et al., 2005a), collectivism–individualism (Triandis et al., 1988), or tightness–looseness (Gelfand et al., 2011a).

These caveats further reinforce the need to understand the origins and function of cross-cultural differences. Disentangling when neurological differences do and do not matter requires the theoretical tools of cultural evolution and the empirical tools of cultural neuroscience. Without cultural neuroscience, cultural evolution remains mind blind. Without cultural evolution, cultural neuroscience continues collecting cross-cultural differences. The confluence of these fields, a cultural evolutionary neuroscience, will give us a more complete understanding of our species.

Chapter 7: Conclusion

The aim of this thesis was to develop a framework for understanding the processes by which cultural evolution contributes to the organisation of the human psychology and behaviour. I did so by conducting theoretical and empirical analysis across the psychobiological domains of genes, internal representations, and the nervous system. In this final chapter I will present an overview that highlights the novel contributions that each chapter has made toward its relevant literature.

Overview of arguments and findings

Chapter 2: General framework

The present thesis brings together two well-established conceptual frameworks, the individual-based framework of the psychological sciences and the population-based framework of cultural evolution. Chapter 2 was a theoretical overview that traces the contours of a synthesis between the two frameworks.

The field of cultural evolution has focused its efforts on describing population dynamics, with less effort devoted to inquiry of the proximate mechanisms, psychological function and its development in particular, that support but are also modified by cultural dynamics. This disparity and the incentive for bridging it have been noted by various researchers. The conventional framework of the psychological sciences is grounded in an individualist approach to the human mind that is philosophically ingrained, methodologically habitualised, and intuitively appealing, but cultural evolution can complement its weaknesses. As cultural evolution offers a rich armamentarium of methods and approaches for dealing with the issues of variation and change, a synthesis between the psychological framework and cultural evolution can facilitate our conceptualisation of variation and change in the psychological domain.

The key point here is that we are not using cultural evolutionary processes as an analogy for understanding psychological processes, but rather as a direct explanation. Because cultural traits make their way into the brain and mind through mechanisms of developmental neuroplasticity, brains and minds are directly shaped by cultural input. Moreover, cultural input is shaped by the population-level dynamics of cultural evolution, which cannot be reduced to an individual-level description. Due to this coupling between the two levels of analysis, the notion of evolvability (Kirschner & Gerhart, 2005; Pigliucci, 2008) transported into the cultural domain serves as a conceptual fulcrum for describing how population dynamics directly govern variation and change in the brain and mind.

Various approaches in developmental science have different ideas about the processes that link developmental inputs to phenotypic outcomes, but what they generally share is the implicit acceptance that the developmental environment is a given: they do not consider the generative processes that dynamically shape environments and thus developmental outcomes. Production of the environment itself is outside the purview of developmental science as it is currently practiced, although approaches such as the bioecological model of human development (Bronfenbrenner & Ceci, 1994a; Bronfenbrenner & Evans, 2000) and probabilistic epigenesis (Gottlieb, 2007) make contact with it. The cultural evolutionary framework is necessary for understanding how, why, and when human environments undergo human-induced change. For humans, the large majority of experience has been channeled by cultural dynamics, and is thus regulated by the past experience (cultural learning) of others. To treat developmental input exclusively as an independent variable is a form of theoretical truncation. A comprehensive explanation of human development requires us to close the loop and describe how developmental outcomes feed into the generation of subsequent environments for subsequent learners. These generative processes arise not from the outcomes of single individuals but rather from population dynamics, making the cultural evolutionary approach to human development a collective approach to phenotypic development.

These points, namely, (1) an enriched approach to the understanding of variation and change in human mental organisation that draws upon the concepts and methods of cultural evolution and (2) a comprehensive framework for capturing the full cycle of human–environment co-production—from the generation of environments, to the effect of those environments on developmental outcomes, to the effect of those outcomes on subsequent environments—are the key theoretical contributions of Chapter 2 and of the overall theoretical framework that guides the discourse of the present thesis.

Chapters 3 & 4: Culture × genetic effects

The conventional nature–nurture framework separates the cause of phenotypic outcomes into those that are innate and those that are acquired, typically mapped onto genes and environment (Dar-Nimrod & Heine, 2011). Therefore, an in-depth analysis of the complex relationship between genes and culture and how to interpret genetic effects in light of this relationship was required, to better understand the critical but commonly neglected role of cumulative cultural evolution in human development. Chapter 3 developed this theoretical framework and Chapter 4 was a pre-registered empirical demonstration of some of its predictions.

Chapter 3: Theoretical contribution

Chapter 3 made theoretical contributions that are relevant for multiple fields including behavioural genetics, cultural evolution, human geography, and developmental science. It focused on the interpretation of heritability, and how it is impacted by cultural dynamics and organisation (e.g., cultural clustering). Behavioural geneticists have long known that heritability can be impacted in subtle ways by events or conditions that affect environmental variance (Charmantier & Garant, 2005; Feldman & Lewontin, 1975; Feldman & Ramachandran, 2018a; Hamer & Sirota, 2000; Haworth & Davis, 2014; Lewontin, 1970a; Moore & Shenk, 2016; Tenesa & Haley, 2013; Turkheimer et al., 2014; Vitzthum, 2003). My co-authors and I reviewed some of these ideas, but our novel contribution to the literature was a description of how the heritability of culturally transmissible traits is expected to change over time as a function of cultural dynamics (as well as how present heritability estimates reflect cultural dynamics that have already run their course). "Culturally transmissible traits" refer to phenotypic traits whose distributions can be shaped by cultural evolution—we postulated that traits in the domains of psychology and behaviour are highly culturally transmissible, while traits in the domains of anatomy and physiology (e.g., the immune, endocrine, circulatory, and digestive systems) would be less (or not) culturally transmissible. More specifically, we offered predictions about how cultural diffusion, cultural innovation, the masking or unmasking of gene function by culture, and changes in the clustering structure of cultural traits will dynamically impact the heritability estimates of culturally transmissible traits over time, along with various empirical examples that illustrate these processes.

In the appendix, we also put forth two formal models—a "variance partitioning model" and a "cultural dynamics model"—that render more explicitly how innovation (or increasing cultural complexity) and diffusion are expected to mediate heritability. The key predictions of the variance partitioning model were that (1) the heritability of a trait will decrease in proportion to cultural variance (i.e., the variability of cultural traits in a society), and that the magnitude of this effect will be dependent on the cultural transmissibility of the trait; and that (2) in societies where the effect of cultural diffusion relative to innovation is high, heritability will tend to be high, while in societies where the relative effect of cultural diffusion is low, heritability will tend to be low. The cultural dynamics model yielded some additional predictions: (3) societies with slow diffusion will on average exhibit lower heritability regardless of whether innovation is rapid or slow; (4) societies with both rapid innovation and rapid diffusion will tend to exhibit short, transient drops in heritability; and (5) societies with slow innovation but rapid diffusion will tend to maintain high heritability. As noted, all of these predictions are for culturally transmissible traits. Rates of innovation and diffusion may not be easy to reliably measure, but they will correlate with features of societies such as cultural tightness/looseness (Gelfand, 2018; Gelfand et al., 2011b), degree of cultural clustering (see Section 3.3.2, "hidden cluster problem"), and the network topology of cultural influence.

Beyond these basic mechanics of culture-induced modulation of heritability, we outlined several methodological problems in the behavioural genetic literature (although not specific to behavioural genetics) that contribute to some of the puzzles, disagreements, and fallacies that exist within the field. One was the "WEIRD sampling problem", which describes a bias in sampling toward highly developed Western countries, which pervades both twin studies and GWAS. This issue is widely recognised (Need & Goldstein, 2009; Polderman et al., 2015b; Popejoy & Fullerton, 2016; Sirugo et al., 2019), but given our proposal that systematic cultural effects shape genetic estimates, the WEIRD sampling problem is likely to be highly detrimental to a sound understanding of the sources of phenotypic variation. A second methodological problem was the "hidden cluster problem". This refers to the recognition that societies vary in the degree to which their cultural transmission networks are fragmented, and that when left unaccounted, this variation renders genetic effects difficult to interpret. A third methodological problem was the "causal locus problem", which describes the additional layers of complexity that gene–culture coevolution brings to the interpretation of genetic effects, and how cultural effects can easily be mistaken as genetic effects and vice versa due to the entangled dynamic between the two. We ended this section with a discussion about a "cultural Simpson's paradox" that arises at the intersection of the three problems, noting how graded degrees of ecological adaptation across societies can cause problems in the statistical interpretation of phenotypic data.

Up to this point, this chapter had focused on general issues that impact all behavioural genetic research. In the subsequent section, we gave predictions and constructed explanations pertaining to long-standing debates in the field of behavioural genetics. These include findings such as differences in heritability across socioeconomic levels, otherwise known as the Scarr-Rowe effect (Rowe et al., 1999; Scarr-Salapatek, 1971; Tucker-Drob & Bates, 2016) (Scarr-Salapatek 1971; Rowe, Jacobson, and Van den Oord 1999); changes in heritability across development for traits such as political orientation (Hatemi et al., 2009) and intelligence (Briley & Tucker-Drob, 2013; Haworth et al., 2010); and the Flynn effect (Flynn, 1984, 1987; Pietschnig & Voracek, 2015; Trahan et al., 2014). We described how each of the above phenomena are respectively explained by variation in the structure of cultural transmission networks across socioeconomic strata; variation in the structure of cultural transmission networks across developmental time, and variation in the structure of cultural transmission networks across historical time. Finally, we outlined some general theoretical implications for how the field of behavioral genetics needs to shift its viewpoint with respect to constructs such as "environment" and intelligence.

This chapter offers a range of contributions, from qualitative predictions about the role of innovation, diffusion, masking, and unmasking; to the description of general methodological problems that affect the interpretation of data; to more fine-grained predictions pertaining to specific puzzles in the behavioural genetic literature. In doing so, we laid out a theoretical framework that is derived from previous work on cultural evolution and gene–culture coevolution but nonetheless offers novel interpretations and explanatory principles that have been tailored to the particular research paradigm of behavioural genetics.

Chapter 4: Empirical contribution

In Chapter 4, my co-authors and I conducted a cross-national analysis to test a prediction we had made in Chapter 3, namely that of a negative association between cultural variance and the heritability of culturally transmissible traits. This was a pre-registered analysis that collected estimates of trait heritability from a comprehensive meta-analysis of twin studies (Polderman et al., 2015b) and estimates of cross-national cultural variance from 3 indices that were constructed on the basis of responses to the World Values Survey and European Values Survey (Inglehart et al., 2014). Two of these were published indices (Uz, 2015), and we constructed a third index that was derived from the methodology of Muthukrishna et al. (2020). Along with the use of 3 indices, we added multiple controls—years of education, population size, and GDP per capita—to check for robustness of results, and employed mixed effects models. We employed an unconventional analytic method due to the expectation of considerable noise in the data. In particular, we preregistered our intention to disregard the use of statistical significance, and to instead rely on the direction of the regression coefficients in a specification curve analysis (Simonsohn et al., 2020) to judge whether the hypothesised relationship was supported.

We did in fact find a largely non-significant but highly robust negative effect of cultural variance with respect to the reported heritability of a preregistered set of psychological, behavioural, and psychiatric traits, which we believed to be culturally transmissible. For the traits that we believed to be less culturally transmissible, there was an effect in the opposite direction. The result was found despite a significant restriction of range in the data, which were collected disproportionately from highly developed Western countries that tend to be clustered toward the high end of cultural variance compared to the global average. We therefore believe that with broader sampling, a larger total effect should become apparent over the expanded range. We also discussed the limitations of relying on country as the unit of analysis, and how it obscures local (sub-national) variation in cultural variance, with implications for how to interpret the findings of the present study.

This chapter makes scholarly contributions in both its methodology and findings. Although specification curve analysis is starting to be employed for topics as diverse as correlates of risk preference (Frey et al., 2021), effects of birth order (Rohrer et al., 2017), effects of digital media on well-being (Orben & Przybylski, 2019), and institutional responses to COVID-19 (Ebersberger & Kuckertz, 2021), it is a new method presumably with various unexplored methods of use. Although our set up of the specification curve was standard, we used it as a method for detecting what we expected to be a faint signal, prioritising uniformity of outcomes over statistical significance. It remains to be seen whether this approach will be considered valid by the research community, but if it is, it may open up a methodological pathway for studying similarly noisy effects.

A second methodological contribution was the construction of a novel index of cultural variance. Although it is similar in many ways to the Uz domain-general index (Uz, 2015) which we also use in the present analysis, the construction of the Muthukrishna index is more transparent due to its code being available online[27].

The primary empirical contribution of this study was the robust finding that heritability does in fact decrease as a function of cross-national cultural variance. This is a novel finding as far as we can tell, and it carries implications for the interpretation of heritability and its relationship to the cultural environment. The finding serves as a verification of some of the key predictions made in Chapter 3 and supports the overall framework. It permits us to commit to further predictions about how heritability will change as a function of changes in cultural transmission within societies, changes in cultural transmission across societies, and changes in the cultural clustering structure of the populations tested, among other parameters.

The theoretical (Chapter 3) and empirical (Chapter 4) components of this project consolidated the full cycle of research inquiry, from (1) discussing a theoretical problem to (2) deriving predictions to (3) designing a methodology for testing the predictions and to (4) verification.

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[27] https://github.com/oritatami/heritability

Chapter 5: Culture × internal representations

If cultural transmission plays a powerful role in the organisation of human minds as I hypothesise, then we should expect to see significant cross-cultural variation in basic features of mental organisation. In Chapter 5, I examined differences in the structure of internal representations across 3 societies.

Although a WEIRD people problem has limited the breadth of the data that are gathered in the psychological and behavioral sciences (Apicella et al., 2020; Barrett, 2020b; Henrich et al., 2010b), recent cross-cultural psychological studies have been steadily cataloguing psychological variation across societies. These include traits that have in the past often been assumed to be universal and culturally invariant, such as memory (Amici et al., 2019; Wang, 2021), visual perception (Kitayama et al., 2003a; Lupyan et al., 2020), event segmentation (Swallow & Wang, 2020b), spatial cognition (Majid et al., 2004), and personality (Gurven et al., 2013). In this chapter I extended this line of inquiry into the domain of internal representations, or more specifically, modalities of thought that people use in their everyday lives such as visual imagery and inner speech. On the one hand, there is a substantial body of work on individual differences in the modality of internal representations (e.g., Kozhevnikov, 2007; Witkin & Moore, 1977), but these studies typically do not look at cultural variation. On the other hand, there is much work on cultural variation in styles of perception (e.g., Kitayama et al., 2003; Masuda & Nisbett, 2001; Uskul et al., 2008) but these studies typically rely on analytic–holistic cognitive style, which is a distinction that occurs within a single representational modality. This chapter fills this gap in this literature.

The structure of internal representations was studied using the recently designed Internal Representations Questionnaire (IRQ; Roebuck & Lupyan, 2020). The original study was conducted on a US sample, where factor analysis was used to derive a 4-factor structure that captured their patterns of responses. The present study administered the IRQ to Chinese participants in the People's Republic of China and Japanese participants in Japan, and is the first cross-cultural study using the IRQ. In particular, I preregistered predictions under the hypothesis that different writing systems would be associated with different structures of internal representation—hence the choice of China and Japan, two societies that employ non-alphabetic systems.

First, a simple comparison of mean scores for each of the 4 factors across the 3 countries revealed salient cross-cultural differences. Compared to the respondents from the original US study, the Chinese and Japanese participants reported considerably higher agreement with items corresponding to orthographic imagery (e.g., "When I hear someone talking, I see words written down in my mind ") and lower agreement with items corresponding to internal verbalisation (e.g., "If I am walking somewhere by myself, I often have a silent conversation with myself").

Several tests including a confirmatory factor analysis suggested that the US factor structure may not be valid for the Chinese and Japanese data. I therefore conducted an exploratory factor analysis for the Chinese data but not for the Japanese data, due to insufficient sample size in the latter. The result was a 3-factor structure that was notably different form the US factor structure. The Chinese factors suggested that some aspects of internal verbalisation are statistically inseparable from orthographic imagery—an outcome that is potentially explained by psycholinguistic and neuroimaging findings about the development of a direct orthography-to-semantics pathway in Chinese readers but not in alphabetic readers, due to material and statistical properties of the Chinese writing system such as a high density of homophony (Cao et al., 2009, 2010, 2014; Perfetti et al., 2013).

In the Chinese factor structure, I also found a potential disjunction between discursive and non-discursive items that both fell under the internal verbalisation factor in the US sample, as well the isolation of a spatial manipulation factor that was a reduced version of the "representational manipulation" factor in the US study. Additionally, I found that male participants had higher factor scores than female participants on the spatial manipulation factor, a conceptual replication of a well-known finding, and that participants who reported more time spent reading had higher factor scores across all factors.

Although preliminary, these findings suggest the presence of meaningful cross-cultural differences in the structure of internal representations. These differences may be associated with the type of orthographic symbols used, where orthographic input during development has downsteream effects on psychological domains beyond writing itself. Written symbols plausibly reorganise internal representations and shape the experience of the way we think, bringing out the question of whether writing may be culturally evolved not just for its commonly assumed functions such as long-range communication and externalised memory, but also for the effects that it has in shaping the totality of our mental lives, in the manner that authors such as Ong (1982) have described.

This chapter does not offer any notable methodological innovations, but its findings agree with the general framework of this thesis. The findings may offer further insight if combined with historical or laboratory studies of the cumulative cultural evolution and diffusion of writing systems, or with sociological analyses of the impact of literacy on thinking and behaviour, for example.

Chapter 6: Culture × brain development

In Chapter 6, my co-authors and I extended the preceding discourse into some of the more concrete organizational features of the nervous system. In particular, the chapter revolved around the disciplinary interface between cultural evolution and cultural neuroscience: a sub-field of cognitive neuroscience that studies cross-cultural variation in neural activity (Chiao et al., 2013). We began by discussing the parallels between the two fields, and the need for cultural neuroscience to adopt a richer and less folk-psychological notion of culture, namely the theoretical framework of cultural evolution.

A theoretical focal point early in the chapter was the relationship between cultural evolutionary flexibility—or evolvability, the capacity of a population to rapidly adapt to environmental change—and neural plasticity. As touched upon in the general framework, neurodevelopmental plasticity is the very medium that allows culturally channeled environmental inputs to shape the psychological and behavioural phenotype. The range of possible phenotypes is therefore dependent upon both the range of flexibility that is inherent in neural systems and the ability of culture to push the brain into ever deeper regions of this neurophenoypic space. Therefore, cultural evolution and neural plasticity jointly support evolvability. Because humans are able to drive forward this process with cultural evolution rather than relying only on genetic evolution, exploration of neurophenotypic space is rapid, and able to proceed in the absence of ecological change. Culture thus serves to shape the nervous system in a flexible manner, and can evolve on the basis of the neurophenotypes that it induces. Many cultural artifacts and practices in fact take the form that they do because they are adapted to the specific characteristics of neural processing. Furthermore, as evolvability is the key property of this culture–brain interface, cross-cultural variation in neurophenotypes serves not just a footnote to WEIRD neuroscience, but rather as a baseline level of analysis of the brain.

We also reviewed the framework of cultural evolution, with a focus on the parallels between genetic and cultural evolution as well as the transmission mechanisms that make high-fidelity learning possible. We then discussed the cultural brain hypothesis, which is a simulation model that captures the coevolution of cultural complexity, brain size, group size, and life history (Muthukrishna, Doebeli, et al., 2018a), synthesing various empirical findings under a cultural evolutionary dynamic.

Most of the latter part of the chapter was devoted to a discussion of the synergistic interaction between large brains and culture. We first broached the problems that come with brain expansion, how it not only incurs an energetic cost but also sets up more possibilities in the processing of sensorimotor input, therefore requiring more efficient methods for searching through this space of configurations. We identified 3 properties of large brains that assist in this search. The first was the organization of the neocortex, whose hierarchical depth scales with brain size (Finlay & Uchiyama, 2015). Deeper hierarchies support more abstract or coarse neural representations, and adaptive representations can be supplied efficiently by cultural transmission. The second property was the longer developmental duration that necessarily accompanies larger brain growth (Workman et al., 2013b). Longer development comes with a greater density of experience, allowing increased cultural influence on the neurodevelopmental process (Finlay & Uchiyama, 2020). Moreover, particular features of brain development such as the protracted maturation of prefrontal cortex may simultaneously support both greater innovation and greater conformity (Chrysikou, Weber, & Thompson-Schill, 2014; Thompson-Schill, Ramscar, & Chrysikou, 2009). The third property we identified was the increased sociality that comes with the energetic requirements of large, immature brains. In the case of humans, this manifests among other things as cooperative parenting, which facilitates social learning (Hrdy, 2011b). Human life history may also be organized around this social environment, with earlier weaning and a long post-menopausal period both supporting transfer of cultural information .

We continued with a discussion of how human brains depend upon others not only for early nutritional support, but also for transmission of cultural knowledge. The functional efficacy of individual brains are therefore intrinsically dependent upon properties of the cultural group such as group size and network topology. Human are equipped with a norm psychology (Chudek & Henrich, 2011) and ethnic psychology (McElreath et al., 2003) that have functional consequences for cumulative cultural evolution, and hence the functional configuration of a population's constituent brains. This discussion converges with the general framework of the present thesis.

The fields of cultural evolution and neuroscience can clearly both benefit from each other's insights, although empirical studies that answer questions in both fields simultaneously may still be difficult. Although there are researchers who study both brain evolution and cultural transmission, explicit integration between cultural evolutionary dynamics and neurodevelopment is still rare, and this chapter attempts to establish an initial convergence.

Synthesis and final remarks

In this thesis, I have assembled an integrative framework that enables productive discourse across cultural evolution, psychology, developmental science, behavioral genetics, and neuroscience. The approach adopted here is grounded in cultural evolutionary theory, but diverges from its disciplinary origins in anthropology and instead prepares it for use in the psychological and behavioural sciences. The individualist philosophy implicit in the theory and practice of human psychology has demonstrated many successes, but it is in need of a more comprehensive reframing that takes into account the generative processes that bring about environmental features that regulate the human mind over its development. What may appear like a self-contained individual trait may in fact be produced through a collective process that spans many generations—a picture that has been obscured by theoretical limitations. Although we understand that things like concepts and languages are assembled collectively and transgenerationally, our limited scope of observation as individuals does not allow us to see this formative process in action, insulating us from a social reality that underpins the individual.

To develop this framework, I have traversed the domains of behavioural genetics, internal representations, and brain development, drawing upon both theoretical and empirical tools. A discussion of genetic effects was necessary in order to clarify the misunderstandings and conundrums that arise in discourse about nature and nurture. This problem has bred misconstrued thinking on this topic not just among laypersons but even among scholars who devote their careers to the study of genes and behavioral development. An integration of behavioural genetics with cultural evolution plays a significant role in resolving this confusion. My co-authors and I have demonstrated that such an integration is is possible, necessary, and surprisingly simple, at least in its principles.

The conventional nature–nurture framework also permeates the fields of psychology and neuroscience, a problem that is exacerbated by a scarcity of cross-cultural data in these fields. The chapter on internal representations served as an example of cultural variation in an aspect of the human mind that many people may consider universal. If a cultural technology like written language reorganises the structure of internal representations, as suggested here, then this opens up both the possibility and incentive for a deeper integration between cultural evolution and the study of cognitive development. The chapter on the neuroscientific implications of cultural evolution consolidated the idea that the brain is a cultural organ powered by population dynamics, going into details pertaining to its development, evolution, and architecture.

Taken in sum, these chapters contest the reductionist view that social and psychological phenomena can be parsimoniously reduced to a genetic or neuronal level of explanation. Cultural dynamics serve as a constituent factor of the functional organisation of brains, minds, and genes associated with psychology and behaviour.

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