Cultural Evolutionary Neuroscience

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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.

Keywords: brain architecture, brain evolution, brain development, Cultural Brain Hypothesis, cultural evolution, cultural neuroscience, cultural transmission, culture–gene coevolution, dual inheritance, human evolution, life history, social learning

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, 2019).

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, Bowerman, Kita, Haun, & Levinson, 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, Chudek, & Henrich, 2018a). Cultural practices such as food sharing (Kaplan, Hill, Lancaster, & Hurtado, 2000a), cooking (Wrangham & Carmody, 2010a), midwifery (Rosenberg & Trevathan, 2002), and modern medical interventions (Lipschuetz et al., 2015) 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, Chudek, & Henrich, 2018b; 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, 1995) 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, 1985b), 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 & Shimojo, 2005; Changizi, Zhang, Ye, & Shimojo, 2006; Vinckier et al., 2007), the structure of speech (Giraud & Poeppel, 2012) as well as every other level of language organization (Christiansen & Chater, 2016; 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, 1995; Navarrete, van Schaik, & Isler, 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, Kuenstner, Mueller, & Huber, 2010), none come as 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, Barnett, Brenner, & Watts-Tobin, 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, Lozupone, Hamady, Knight, & Gordon, 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, 2017; Laland et al., 2015).

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, Bekkering, & Kiraly, 2002; Horner & Whiten, 2005; Lyons, Young, & Keil, 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, Melis, Tennie, Wyman, &

Herrmann, 2012; Wilson, 2012) and life history (Gurven, Kaplan, & Gutierrez, 2006a; Schniter, Gurven, Kaplan, Wilcox, & Hooper, 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, 1981). 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, Strimling, Eriksson, Laland, & Sjostrand, 2010). 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, Tracy, Foulsham, Kingstone, & Henrich, 2013; Chudek, Heller, Birch, & Henrich, 2012; Joseph Henrich & Gil-White, 2001), 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, 1995; Joseph Henrich & Boyd, 2008; Kuzawa et al., 2014; Leonard, Robertson, Snodgrass, & Kuzawa, 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, 2011; Kaplan, Hill, Lancaster, & Hurtado, 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., 2006a; Koster et al., 2019; Schniter et al., 2015a; Schuppli, Isler, & Van Schaik, 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 & Shultz, 2007; Dunbar, 1992), 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, Williams, & Higham, 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 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.

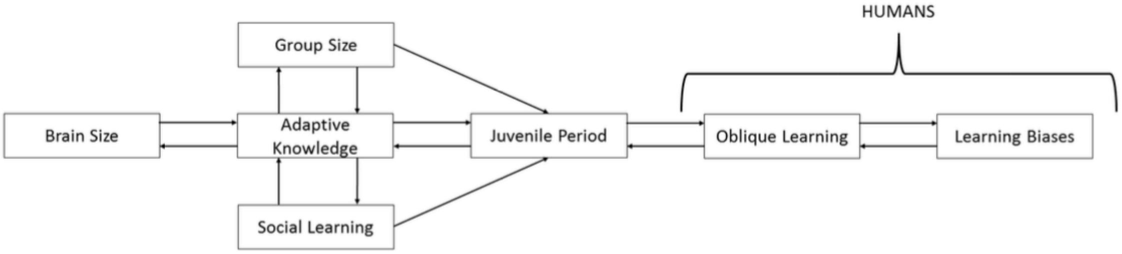

Figure 1: Causal relationships predicted by the Cultural Brain Hypothesis (adapted from Muthukrishna et al., 2018)

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, Merola, & Basarab, 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, Thompson, & Rosch, 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, Bengio, & Hinton, 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, Zoccolan, & Rust, 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 caudal-to-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, Harrison, & Penny, 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, Reddy, Kreiman, Koch, & Fried, 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, Nestor, & Rogers, 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, Bazin, & Margulies, 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, Mar, & Kim, 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, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 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, Vanderwal, & Hasson, 2019; Simony et al., 2016; Zacks, Speer, Swallow, & Maley, 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., 2013). 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 (Gottlieb, Keydar, & Epstein, 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., 2013).

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, Brown, & Enquist, 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, Bridgers, Griffiths, & Gopnik, 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, Young, & Keil, 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, Aihara, Aoki, Araki, & Nakazawa, 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, 2011). 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 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, 2011). 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., 2018b; 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 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, Kaplan, & Gutierrez, 2006b; Schniter, Gurven, Kaplan, Wilcox, & Hooper, 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 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., 2018b) 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).

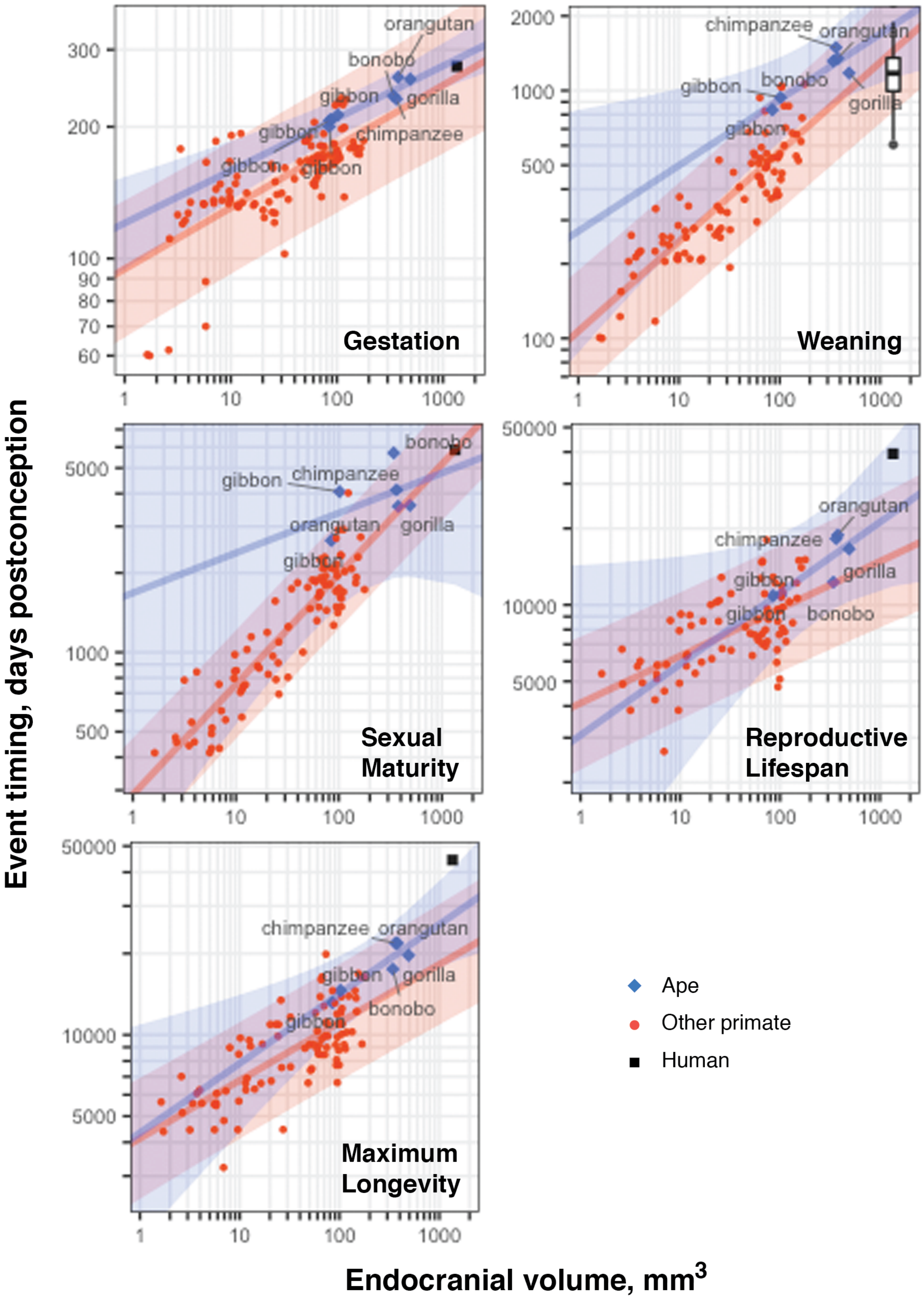
Event timing, days postconception
Endocranial volume, mm^3
Gestation
300
200
100
90
80
70
60
1
10
100
1000
orangutan
bonobo
gibbon
gorilla
gibbon
chimpanzee
gibbon
gibbon
Weaning
2000
1000
500
100
chimpanzee
orangutan
gibbon
bonobo
gorilla
gibbon
Sexual Maturity
5000
1000
500
bonobo
gibbon
chimpanzee
orangutan
gorilla
gibbon
Reproductive Lifespan
50000
10000
5000
orangutan
chimpanzee
gibbon
gorilla
gibbon
bonobo
Maximum Longevity
50000
10000
5000
chimpanzee
orangutan
gibbon
gorilla
bonobo
gibbon
◆ Ape
● Other primate
■ Human

Figure 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, Beugin, Godelle, & Raymond, 2013; Derex & Boyd, 2016; Goldstone & Theiner, 2017; J Henrich, 2004; Muthukrishna & Henrich, 2016b; Muthukrishna, Shulman, Vasilescu, & Henrich, 2013). 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, Boyd, & Richerson, 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, Shennan, & Thomas, 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, Price, Flandin, & Friston, 2006; Noppeney, Price, Penny, & Friston, 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, Sporns, & Edelman, 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; 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, Friston, & Price, 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., 2017; Coan, Schaefer, & Davidson, 2006), or is likely to have performance implications, such as the relationship between age and brain structure (LeWinn, Sheridan, Keyes, Hamilton, & McLaughlin, 2017), reading and writing (Bolger, Perfetti, & Schneider, 2005; Kobayashi, Glover, & Temple, 2007; Tan, Laird, Li, & Fox, 2005), collectivism–individualism (Triandis, Bontempo, Villareal, Asai, & Lucca, 1988), or tightness–looseness (Gelfand et al., 2011).

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.

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