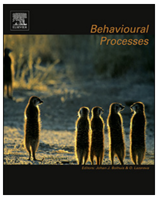
Behavioural Processes 161 (2019) 73–86

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Pathways to cognitive design

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ARTICLE INFO

Keywords:
Natural selection
Genetic evolution
Cultural evolution
Plant cognition
Symbolic group boundary cognition

ABSTRACT

Despite a shared recognition that the design of the human mind and the design of human culture are tightly linked, researchers in the evolutionary social sciences tend to specialize in understanding one at the expense of the other. The disciplinary boundaries roughly correspond to research traditions that focus more on natural selection and those that focus more on cultural evolution. In this paper, we articulate how two research traditions within the evolutionary social sciences—evolutionary psychology and cultural evolution—approach the study of design. We focus our analysis on the design of cognitive mechanisms that are the result of the interplay of genetic and cultural evolution. We aim to show how the approaches of these two research traditions can complement each other, and provide a framework for developing a wider range of testable hypotheses about cognitive design. To do so, we provide concrete illustrations of how this integrated approach can be used to interrogate cognitive design using examples from our own work on plant and symbolic group boundary cognition. We hope this recognition of different pathways to design will broaden the hypothesis space in the evolutionary social sciences and encourage methodological pluralism in the investigation of the mind.

1. Introduction

In the mid-19th century, Darwin and Wallace independently realized how natural selection can give rise to functional adaptations that look well-designed for particular functions in organisms (Darwin, 1859; Darwin and Wallace, 1858). Later, in the second half of the 20th century, theoreticians started developing models showing that cultural traits could spread in ways analogous to natural selection and result in well-designed institutions and technologies, such as writing systems, calculators, and constitutional systems of government over the course of multiple generations (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Pulliam and Dunford, 1980). Since that time, there has been debate concerning how to integrate theories of natural selection, which generally emphasize the process of genetic evolution, and cultural evolution. In this paper we explore the scientific consequences of recognizing both of these evolutionary processes for the evolutionary social sciences, particularly those focused on cognition. We have three main goals: (1) to outline the consequences of the de facto split between research traditions that emphasize genetic and cultural selection to different degrees for investigations of human cognitive architecture, (2) to encourage the exploration of a broader hypothesis space that considers the ways that genetic and cultural evolution can produce functional cognitive design, and (3) to illustrate how diverse lines of evidence contribute to our understanding of the evolution of the mind.

We begin in Section 1.1 with brief overviews of two approaches within the evolutionary sciences: evolutionary psychology and cultural evolution. We then outline some apparent dichotomies between the two approaches and, in Sections 1.2 and 1.3, suggest some ways in which the existing gaps can be bridged. While we will not propose a unique theoretical or methodological approach in this paper, we hope to shed light on how the different research approaches can complement each other (Kolodny et al., 2018; Smith, 2000) and provide frameworks for developing and testing a wider range of hypotheses about cognitive design.

Section 2 describes some principles that can guide researchers in assessing whether a domain of psychological design is likely to be the product of both cultural and genetic evolution. These guidelines clarify the ways and reasons why the processes of genetic and cultural evolution become entwined.

Then, in Section 3, we provide concrete illustrations of how to develop and test a broader set of evolutionary hypotheses using examples from our own work investigating the cognitive design for learning about plants (Wertz) and symbolic group boundaries (Moya). We come from different research traditions that emphasize the roles of genetic and cultural evolutionary processes to cognitive design to different degrees, and we have found that our meta-theoretical views have been sharpened and strengthened through engaging with one another's disciplinary assumptions and insights. We attempt to move down a level of

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https://doi.org/10.1016/j.beproc.2018.05.013
Received 31 August 2017; Received in revised form 1 May 2018; Accepted 22 May 2018

abstraction and apply what we have each learned from these different research traditions to our own research programs. We hope to provide more concrete paths forward for those facing the same challenge of understanding how cognitive mechanisms show functional design. Some aspects of what we discuss about our own research will be backed up by empirical data we have already collected, while other aspects will be more speculative.

1.1. Divergent research traditions in the evolutionary social sciences

There are several research traditions within the evolutionary social sciences each with its own methods and ontological commitments, but here we focus on two: evolutionary psychology and cultural evolution. We will not dwell on disagreements between the two research traditions, even though they have often been at odds with each other. This is not meant to suggest that the reasons for the disagreements are trivial or unworthy of further argument and debate. Differences persist between the fields in their meta-theoretical approaches and notions of critical concepts (e.g., domain specificity, Cosmides and Tooby, 1994; group selection, Richerson et al., 2016), but resolution of those debates is beyond the scope of any one paper. Our aim here is instead to provide an overview of how these fields currently investigate human cognition and suggest some paths forward for their integration.

Evolutionary psychology uses principles of natural selection to predict (or explain) aspects of human cognitive architecture (e.g., Barrett, 2015; Cosmides and Tooby, 1987, 1994; Daly and Wilson, 1988; Lewis et al., 2017; Tooby and Cosmides, 1990, 1992; Tooby and Cosmides, 2015). The research is largely focused on interrogating the structure of cognitive mechanisms and primarily uses research methods from the field of psychology. The empirical investigations have pursued diverse aspects of human cognitive architecture, including the structure of reasoning and decision making algorithms (Cosmides, 1989; Cosmides et al., 2010; Gigerenzer et al., 1999; Tan et al., 2017), coalitions (Cosmides et al., 2003; Pietraszewski, 2016; Pietraszewski et al., 2014), mate choice (Buss, 1989; Conroy-Beam and Buss, 2016; Thornhill and Gangestad, 1999), social behavior and motivations (Neuberg and Schaller, 2014; Neuberg et al., 2010), kin recognition (Lieberman et al., 2007), personality (Lukaszewski and von Rueden, 2015), foraging (Krasnow et al., 2011; Wilke and Barrett, 2009) and emotions (Sell et al., 2009; Tybur et al., 2013) among many others (see e.g., Buss, 2015).

The field of cultural evolution examines the patterned ways that cultural traits such as beliefs, technologies, and institutions change through time and across populations, and how this impacts human behavior and the structure of human societies. The research focus has largely emphasized mathematical models of evolutionary dynamics (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Panchanathan and Frankenhuis, 2016), experimental social learning work (Mesoudi and Whiten, 2008; Derex and Boyd, 2016), and methodologically plural cross-cultural empirical projects about behavior (Colleran et al., 2014; Henrich et al., 2001; Mathew and Boyd, 2014), cognition (Moya et al., 2015; Kline et al., 2018), institutions (Turchin et al., 2013; Mace and Holden, 2005), and material culture (Shennan, 2002; Perreault, 2012).

These differences correspond roughly to one research area focusing more on psychology as an individual-level structure and the other focusing more on culture as a population-level structure. To be clear, neither research tradition advocates viewing human psychological architecture as being independent of, or in opposition to, human culture (Boyd and Richerson, 1985; Tooby and Cosmides, 1992) and research in certain areas is already blurring these disciplinary lines. For example, practitioners from various evolutionary social science fields address questions about cooperation and morality (Barclay and Raihani, 2016; Delton et al., 2012; DeScioli and Kurzban, 2009; Panchanathan and Boyd, 2004; Richerson et al., 2016; Hoffman et al., 2016) social learning (Barrett and Broesch, 2012; Kline, 2015; Wertz and Wynn, 2014a), and intergroup relations (Neuberg and DiScioli, 2015; Moya and Boyd, 2016; Pisor and Gurven, 2016). This dissolution of boundaries is particularly apparent regarding cross-cultural cognitive and behavioral economic work (Barrett and Broesch, 2012; Barrett et al., 2016a,b; Buss, 1989; Purzycki et al., 2016; Sznycer et al., 2017). However the typical division of labor has the unfortunate consequence of researchers in each tradition effectively black-boxing or, at times, denying the contributions of the other.

Further, the two research traditions tend to conceptualize evolutionary dynamics in slightly different terms. Evolutionary psychologists focus on the process of "natural selection," through which the dynamics of differential reproductive success create organismal design around recurrent features of the environment (e.g., Barrett, 2015; Tooby and Cosmides, 1992, 2015). Cultural evolutionists, on the other hand, make a distinction between the design-building processes of "genetic evolution" and "cultural evolution" because of the differences in transmission pathways they allow (e.g., Boyd and Richerson, 1985; Richerson and Boyd, 2005). In this research tradition, the label "natural selection" is often used to denote a process that favors traits that affect the differential reproductive success of their hosts, regardless of a trait's genetic or cultural transmission pathway (Rogers and Ehrlich, 2008). This is not to say that cultural evolutionists view genetic and cultural evolutionary processes as separate. In fact, the entire research enterprise of gene-culture coevolution is devoted to examining the ways in which the two processes interact over different intergenerational timescales (e.g., Boyd and Richerson, 1985; Durham, 1991; Chudek and Henrich, 2011). Somewhat analogously, evolutionary psychologists subsume the cultural environment under the broader conceptualization of recurrent aspects of the environment on which selection can act (Barrett, 2015; Tooby and Cosmides, 1992, 2015).

The different use of terminology follows from the research foci of each field, but (as we have found while writing this paper) it can cause quite a lot of confusion. In the sections that follow, we have attempted to describe the abstract dynamics affecting the evolution of human cognition using terminology that is accessible to both research traditions in an effort to build some bridges between them. We recognize that this attempt runs the risk of irritating practitioners on both sides of the traditional theoretical divide, but we do not intend this articulation to be the final word on the subject. Instead, we offer this initial attempt as a path forward on which others might build.

1.2. Design: some common ground

One fundamental similarity between these traditions is their focus on predicting and explaining functional *designs*. As we outline above, to a first approximation, evolutionary psychology focuses more on the contributions of natural selection (with an emphasis on genetic evolutionary processes) to design, and cultural evolution focuses, as its name suggests, more on the contributions of cultural evolutionary processes to design. The concept of "design" has been used in many ways in the past, so we will briefly clarify our meaning here. If organisms vary on a trait that contributes to differential abilities to successfully reproduce, and that trait can be transmitted to the next generation, the trait will, all else equal, increase in frequency over time. Over generations the accumulation of such traits can lead to *designs* that are competent at surviving and reproducing in a given environment, and can produce increasingly tight fits between form and function (see Dennett, 1995; Gardner, 2009; Grafen, 2007; Stearns, 1977; Williams, 1966; for more exhaustive treatments). In short, *design* is structure that is well-suited to solve a problem.

Darwin had this insight about design after engaging in extensive comparative natural history work (Darwin, 1845, 1859) and the now iconic finches he collected while visiting different islands in the Galapagos serve as a good example. The birds on each island originated from the same ancestral finch species, but later possessed systematically different traits. Specifically, the finches on different islands had different beak shapes that possessed design features well-tailored to the different food sources the birds exploited on their island. For example, one type of finch fed on hard seeds and had a correspondingly shorter and more powerful beak, while another fed on insects plucked from bark and other vegetation and had a much thinner pointed beak. These different designs reflect the fit between form and function that is produced by natural selection, even though other neutral evolutionary processes and constraints affect how tightly a phenotype fits a function.

Evolved designs are necessarily contingent on features of the environment, including variable features of the environment. For example, the tadpoles of spadefoot toads (*Scaphiopus multiplicatus*) develop in small ponds. These small ponds are prone to evaporation at variable rates, which has consequences for the timing and manner of the spadefoot tadpoles' development. In response to these variable conditions, this species has evolved two morphs of tadpoles that develop at different rates and exploit different food resources. There is a slower developing, smaller, omnivorous morph that eats the detritus in the pond, and a faster growing, larger, carnivorous morph that eats the small shrimp also found in the pond, and sometimes the other (usually unrelated) tadpoles as well (Pfennig, 1990a,b, 1992a). The carnivorous morph is triggered by the ingestion of a shrimp–an event which is correlated with pond evaporation rates (Pfennig, 1990a)–and switches back to the omnivorous morph if the tadpole no longer consumes large prey (Pfennig, 1992a,b). In this way, spadefoot tadpoles adjust their developmental trajectory to cope with the variable conditions afforded by small ponds. As this example illustrates, biological design can respond contingently to variable environmental conditions over evolutionary times scales (i.e., the evolution of two tadpole morphs) and also over developmental time scales (i.e., the switch between omnivorous and carnivorous morphs over a single lifetime).

These insights about the evolution of design are, of course, not limited to birds and toads, but apply to all aspects of biological design, including the human mind (Barrett, 2015; Buss, 2015; Cosmides and Tooby, 1987, 1994; Daly and Wilson, 1988; Lewis et al., 2017; Tooby and Cosmides, 1990, 1992, 2015). Indeed, as the diverse research programs mentioned in Section 1.1 above demonstrate, there is now considerable evidence that the design of the human mind reflects the structure of the recurrent adaptive problems humans faced.

While the process of accumulating designs is typically defined as natural selection when the units of inheritance are genes, Darwin had this insight with no understanding of the inheritance mechanism and the same set of assumptions can be applied to traits that are transmitted culturally between individuals. There is a lively debate about the extent to which cultural and genetic evolutionary processes resemble each other (Acerbi and Mesoudi, 2015; Aunger, 2001; Blackmore, 2008; Boyd et al., 2011; Claidière et al., 2014; Claidière and Sperber, 2007; Kundt, 2017; Mesoudi, 2017; Pinker, 2010), but our goals here do not require a particular stance on most of these issues. In the case of cultural evolution the same principle holds that the traits that have features that increase their transmission probability will similarly increase in frequency.

Cultural inheritance opens up more mechanisms of transmission. Most similar to genetic natural selection, cultural traits may improve the survival and biological reproduction of the people who have those traits. However, cultural traits that are better *designed* to make learning them easy, or better *designed* to make those who have them succeed (and therefore deemed worthy of copying), are also more likely to be transmitted, even among genetically unrelated individuals. These different inheritance mechanisms set the stage for distinct evolutionary processes. What makes a cultural trait easier to learn, or a person successful and therefore worth copying, will necessarily, but not exclusively, depend on the genetically-evolved designs of the human mind. This means that not only is the capacity to learn from others a product of natural selection, but the form that successfully transmitted cultural traits will take is informed by genetically-evolved cognitive mechanisms.

However, understanding the design of the human mind exclusively in terms of genetic evolutionary processes is nevertheless insufficient for understanding the form that cultural traits will take. For example, it would be nearly impossible to understand the origins and development of canoe-making without further information about population-level characteristics such as the ecology, social network structures affecting learning opportunities, extent to which people specialize in certain skills relevant to canoe building, and the available tools and materials for constructing a canoe. Such information is necessary for understanding the psychological adaptations that allow people to become competent canoe makers and users. This is because institutions, tools, and other cultural features of a society can directly influence the design of the cognitive architecture responsible for canoe building and use over multiple generations, as well as how the relevant cognitive systems develop over an individual's lifetime. For example, methods of teaching canoe skills can themselves be products of intergenerational, and cumulative, cultural evolutionary processes that produce better **designed** (e.g., more effective) ways of teaching (Kline, 2015). Who teaches canoe building skills, the sequence in which skills are taught, and the ages at which children start to learn about canoe building are just some components of culturally-evolved teaching complexes that can directly influence the development of cognitive mechanisms over the course of individual's lives, and intergenerationally.

This example illustrates not only that (1) technologies and institutions, like teaching methods, can be conceived as designs produced by intergenerational ratcheting of complex cultural traits (i.e., cumulative culture) that no single individual could have created on their own (Boyd et al., 2011), but that (2) cognitive mechanisms that are well-designed for interacting with culturally-constructed worlds (e.g., for canoe building, maneuvering, and navigating) are likely products of both genetic and cultural evolutionary processes.

1.3. *Conceptual integration*

The common ground of focusing on *design* provides hope that different research traditions can be brought together, but it creates practical problems for cleanly identifying the source of any particular piece of cognitive design. Although it is more conceptually tractable to view genetic and cultural processes as separate, in reality their effects can never be fully disentangled because the two processes interact. Genetic selection and cultural evolution are nested processes unfolding over both phylogenetic (long-term evolutionary) and ontogenetic (developmental) timescales. Minimally, aspects of human phenotype that are involved in the generation, acquisition, and transmission of culture are necessarily the product of their interaction.

To see why this must be the case, we will briefly sketch out ways in which genetic and cultural evolution are linked over phylogenetic and ontogenetic time. The insights we will outline are not new. The tight link between culture and evolved psychology is a foundational tenet of the research traditions that focus more on natural selection (genetic evolution) and those that focus more on cultural evolution (Boyd and Richerson, 1985; Durham, 1991; Sperber and Hirschfeld, 2004; Tooby and Cosmides, 1992). Furthermore, the interplay of genetic and cultural evolution is the explicit focus of the field of gene-culture coevolution (Boyd and Richerson, 1985; Chudek and Henrich, 2011; Durham, 1991; Henrich, 2015; Laland et al., 2010; Lotem et al., 2017; Moya and Henrich, 2016). We outline that interplay here.

When viewed through a phylogenetic lens, the generation and acquisition of cultural information must have initially been made possible by cognitive mechanisms that arose via genetic selection. Culture cannot occur unless there is a psychology capable of supporting it (Barrett, 2015; Boyd and Richerson, 1985; Henrich and McElreath, 2003; Laland et al., 2000; Tooby and Cosmides, 1992). Many organisms have mechanisms for learning from others (Hoppitt and Laland, 2013), and transmitting skills and information to others (Kline, 2015). However, intergenerational ratcheting of socially-acquired information to produce complex cultural systems maintained over long timescales and large populations is vanishingly rare, and likely currently unique to humans (Richerson and Boyd, 2005).

The particular suite of cognitive and other phenotypic adaptations that initially arose and enabled hominins to generate and acquire cultural information is debated (Hoppitt and Laland, 2013; Moya and Henrich, 2016; Rendell et al., 2011). However, once such mechanisms became part of human cognitive architecture, they gave rise to the cultural evolutionary dynamics that henceforth changed the human environment by introducing culturally-evolved designs. At one level, over ontogenetic time, aspects of human cognitive architecture could then develop through the interaction of these new kinds of cultural environments and genetic adaptations. At another level, the presence of cultural information—including, for example, traditions, institutions, and tools—itself becomes a recurrent feature of the human selective environment. This means that genetic selection can further shape cognitive mechanisms around the presence of cultural information. Further, at both levels, the structure of the cultural information is itself a product of the structure of the psychological mechanisms that give rise to it through their interaction with the environment.

The consequences of these co-evolutionary processes for understanding the structure of human cognition is well illustrated by the case of language acquisition psychology. Language acquisition serves as a useful case study because human psychology contains evolved cognitive capacities that allow individuals to acquire any human language depending on the linguistic environment that they are exposed to, and because different human cultures have evolved thousands of variable languages. Furthermore, there is a large and well-developed language acquisition and evolution literature from which to draw relevant empirical evidence. Finally, language is a domain for which there is broad consensus among most evolutionary social scientists that both genetic and cultural evolutionary processes account for the design of modern human communication systems (e.g., Christiansen et al., 2009; Everett, 2012; Pinker, 2003; Tamariz and Kirby, 2016).

First, the example of language illustrates that certain cognitive adaptations have been designed over phylogenetic time to depend on the presence of cultural information to develop over ontogenetic time. If the expected linguistic input is not received by a certain point in development, the cognitive mechanisms do not produce full linguistic competences, and the competences that are produced remain impaired even when language input is provided later in life (Fromkin et al., 1974; Johnson and Newport, 1989). This means that the language acquisition mechanisms themselves are designed to expect the cultural input of being exposed to language. Further, these adaptations develop contingently based on the structure of the social inputs received from speakers of culturally-evolved languages. The contingent development of linguistic skills is reflected in phoneme narrowing (Werker and Desjardins, 1995; Werker and Tees, 1984), and the acquisition of diverse grammatical structures and lexicons (Pinker, 2003; Pinker and Bloom, 1990).

Second, the language case study illustrates that functional cultural traits are not restricted to the material domain (e.g., arrow heads and canoes). Rather, ways of communicating can themselves be considered technologies that culturally evolve to be efficient and effective (Everett, 2012). Languages change at a rapid pace—American English today is certainly not the same as English spoken 500 years ago and is noticeably different than American English spoken just a few decades ago (e.g., one doesn't hear things described as "Swell!" much anymore). Such shifts can include functional changes in language that facilitate communication, or thinking novel thoughts (Deutscher, 2005, 2010). For example, the way that linguistic terms map onto representations of quantity varies across language systems. In some languages, numerical systems do not have concepts of zero or of exact quantities more generally, and different linguistic systems facilitate arithmetic manipulations to different degrees (Frank et al., 2008). Even though all humans have the capacity to acquire any of these numerical systems, individuals who develop within these different culturally-evolved linguistic environments exhibit cognitive design that corresponds to the local cultural environment.

At this point, it should be clear that the processes of genetic and cultural evolution are inextricably linked, such that it is no longer truly possible to fully disentangle the contributions of these two processes to current manifestations of design produced by their interaction. And yet, as the language acquisition example illustrates, it remains possible, and indeed necessary, to consider the contributions of each process to come to a full understanding of the design of human cognition.

The way forward is challenging. There is no checklist of features that will allow us to cleanly identify the type of designs produced by genetic or cultural evolution. In addition to the fact that both processes are tightly linked, both design-producing processes produce a fit between form and function, as we have outlined above. This means that the structure of the design produced will be dependent on the particular function the design serves, no matter which process is in play. It is therefore impossible to point to an aspect of phenotype and state that because it genetically evolved, it must have feature X or that because it culturally evolved, it must have feature Y. Put simply, if one is attempting to predict (or explain) aspects of design, the only rule of thumb that will apply in all circumstances is "it depends" (Barrett, 2015).

Instead, the empirical path towards integrating these conceptual insights about the entwined nature of genetic and cultural evolutionary processes involves pushing aside divisions between disciplinary camps to incorporate insights from each field into our hypothesis development. The de facto disciplinary boundaries between those primarily researching psychological architecture through the lens of (usually genetic) natural selection and those who study the structure and development of culture discourages tests of a wider range of hypotheses about the design of the human mind. This does not have to be the case. For example, researchers coming from a more traditional evolutionary psychology approach might consider whether some feature of the cognitive architecture that looks well-designed could have arisen through the acquisition of culturally-designed ways of thinking. This goes beyond the initial step of recognizing that culture influences cognition, to thinking about cultural processes as sources of design. Because cultural evolution produces ordered informational structures, practices, and institutions that are an important part of recurrent human environments, serious considerations of these dynamics can suggest more precise hypotheses about both the inputs to certain kinds of cognitive mechanisms, as well as more precise hypotheses about the structure of the psychological architecture that interfaces with those inputs.

Researchers coming from a more traditional cultural evolutionary approach might consider whether their hypotheses provide a full accounting of the genetically-evolved cognitive mechanisms that would be necessary for a proposed socially-learned trait to be acquired. Similarly, this requires a deeper resolution beyond acknowledging that evolved motivations or cognitive biases influence the form of cultural content, to recognizing that culture acquisition capacities require complex psychological adaptations. Genetic selection produces functionally organized cognitive architecture, whether or not cultural selection plays a role. Given the phylogenetic recency of complex cultural adaptations, it is exceedingly unlikely that human cognition can be understood through cultural evolution alone, even in cases where adaptive features of psychological structures are largely products of cultural selection. Taking seriously the interaction of genetic and cultural evolutiona in structuring psychological adaptations can suggest more precise hypotheses about the form that certain cultural adaptations take and the dynamics of how they are transmitted.

After developing a richer, and hopefully more accurate, set of hypotheses from this more integrated approach, we face the challenge of empirically evaluating them. In Section 3 we describe this process with illustrations from our own work. But first we give some guidelines about the domains of cognition that we think would particularly benefit from this integrated approach.

2. For what kinds of cognitive mechanisms is this kind of analysis useful?

Theoretical work on the types of adaptive challenges and environments that favor social learning and cultural evolution can inform when this integrated approach will be particularly useful. At a broad level, any cognitive mechanism that makes use of socially learned information or cultural products is likely to have design features produced by the joint operation of genetic and cultural evolution. We briefly elaborate on three principles that can help us identify such cognitive mechanisms: (1) Is the adaptive problem one that varies considerably across time and space?, (2) Is individual learning within the domain of the adaptive problem costly or difficult?, and (3) Is the cognitive mechanism one whose benefit depends on its frequency within a population? We elaborate on each of these principles below.

2.1. Is the adaptive problem one that varies considerably across time and space?

Cognitive mechanisms that make use of socially learned information or cultural products are favored by natural selection under circumstances where the relevant environmental conditions vary at intermediate time scales, particularly in novel ways (Boyd and Richerson, 1985). This means that an individual would face an unknown environment, while a population composed of people from different generations may have accumulated some knowledge of the environmental condition over a longer time scale. Under such circumstances, a canalized strategy that does not respond flexibly to changing circumstances will be outcompeted by one that learns by taking input from the social or cultural environment and responds contingently.[1] Furthermore, a strategy that only relies on individual experiences would be outperformed by one that takes advantage of the cultural information stored in the population. Conversely, if the environment is very stable, natural selection can favor a genetic adaptation that reliably develops in a canalized fashion with little environmental (including cultural) input. If the environment changes very quickly, population level knowledge may quickly become misleading and outdated.

For example, there is good evidence that the phonemic repertoires that human languages use vary geographically (Dryer and Haspelmath, 2013) and temporally at broad intergenerational time scales (Perreault and Mathew, 2012). This suggests that social learning algorithms will be necessary for individuals to acquire the phonemes for their local environment from others. Correspondingly, there is evidence that human infants are born being able to discriminate all phonemes used in human speech, but preferentially attend to the sounds of their native language (e.g., Jusczyk et al., 1993) and, between 6–12 months of age, their phonemic repertoire narrows to the phonemes they experience in their local culture (Kuhl, 2004; Werker and Tees, 1984).

2.2. Is individual learning within the domain of the adaptive problem costly or difficult?

Second, cognitive mechanisms that make use of socially learned information or cultural products will be particularly useful when individual learning strategies, such as trial and error learning, are difficult or costly (Boyd and Richerson, 1985). Findings across the animal world confirm the existence of strategies matching this prediction. For example, birds learn about patch quality from others when this information is difficult to discern asocially (Templeton and Giraldeau, 1996). In the domain of communication, Laland (2004) suggests that predator alarm systems are common precisely because of the costs of individual learning in this domain.

2.3. Is the cognitive mechanism one whose benefit depends on its frequency within a population?

Third, cognitive mechanisms that make use of socially learned information or cultural products are likely to be in play if the fitness consequences of a trait depend on how many other individuals in a population behave the same way. This is because critical information must be gleaned from others in order to coordinate with them (McElreath et al., 2003). Such coordination and information sharing is even more important if the behavior in question is incentivized because of its reputational consequences (Boyd et al., 2010; Nowak and Sigmund, 2005). Communication systems as a whole are a good example of a suite of traits whose payoffs depend critically on coordinating with others. There is no point to yelling, “look out!” if no one can understand you, and no point to understanding this phrase if no one uses it. Coordinated communication systems do arise through genetic evolutionary processes (e.g., as is the case with many non-human signaling systems; see Seyfarth et al., 1980). However, human languages vary across genetically equivalent populations, indicating that people coordinate on different communication systems through social learning. As models of the formation of new languages demonstrate, the benefits of using a particular communication system depend on how many others do so (e.g., creole languages; Jansson et al., 2015).

These three principles describe many of the features of the adaptive challenges related to our own research programs: learning about plants (Wertz) and symbolic group boundaries (Moya). First, the plants and symbolic groups that humans faced likely changed over evolutionary time, across environments, and according to local socio-ecologies. Second, certain kinds of interactions with novel (potentially toxic) plants or (potentially dangerous) strangers were likely to benefit from social information rather than individual experimentation. Third, the benefits of seeking certain plant foods (e.g., ones that benefited from coordinated foraging) or interacting with certain social groups (e.g., in contexts where one does not want to be outnumbered by an outgroup) likely depended on how many other people engaged in the same behavior. We continue by illustrating how to use lines of evidence that focus on different time scales—from phylogenetic to historical to developmental—to elucidate the joint influence of cultural and genetic evolutionary processes on the design of the mind in these domains.

3. Illustrations

We use two case studies to illustrate the challenges and opportunities presented by considering the different mechanisms that can give rise to cognitive design: learning about plants (Section 3.1) and learning about symbolically-marked group boundaries (Section 3.2). For each case study we begin by describing the adaptive problem(s) under investigation. We then propose possible design features of the cognitive mechanisms that could arise from the interplay of genetic and cultural evolutionary pathways to help solve those problems, and discuss the empirical data to date that speak to these proposals. Table 1 summarizes some of the kinds of evidence that we draw on for each of these domains. These illustration sections are not meant to be exhaustive reviews or defenses of the proposed adaptive problems or cognitive design. Instead, throughout each illustration, we highlight the aspects of design that typically follow from the foci of the two research traditions—evolutionary psychology and cultural evolution—in order to provide concrete examples of how considering a wider hypothesis space about design origins can facilitate and strengthen research programs investigating the structure of the human mind.

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[1] We restrict ourselves here to the focused topic of input from the social / cultural environment. Of course, similar principles apply for the evolution of individual learning (see Boyd and Richerson, 1985; Richerson and Boyd, 2005) and phenotypes that respond contingently to the environment via other mechanisms (see e.g., Barrett, 2005; Richerson, this special issue; Tooby and Cosmides, 1990; Tooby et al., 2003).

Table 1
Summary of evidence relevant to understanding pathways of design. Each row represents a different cognitive domain–plants or symbolically marked group cognition. Evidence is categorized by columns representing different kinds of data relevant at different timescales–ordered from the most distal (phylogenetic) to the most immediate (ethnographic). Evidence lists are illustrative rather than exhaustive.

		Evidence			
		Phylogenetic	Historical	Developmental	Ethnographic
Domain	Plants	1. Physiology and behavior of animals from insects to apes includes design for consuming plant material (morphology, enzymatic detoxification pathways, foraging strategies, etc.) 2. Archeological evidence of plant consumption throughout hominin lineage 3. Plant processing techniques used by many monkey and ape species 4. Evidence that nonhuman animals (e.g., sheep and bees) categorize plants	1. Evidence of plant consumption and processing in ancient human populations (~10,000 years) 2. Evidence of ancient plant–based tools (e.g., rope)	1. Infants exhibit behavioral avoidance of plants compared to control entities matched along dimensions of perceptual similarity, familiarity, and natural-occurrence 2. Infants selectively learn plant edibility from social cues 3. Foraging for or tending to plants begins around 2-3 years of age in some subsistence societies	1. Plant calories account for between 10-70% of modern hunter-gatherer diets 2. Plants that are toxic or suboptimal if not processed are commonly consumed 3. Plant materials used to construct artifacts (e.g., tools, shelters) 4. Plant chemicals exploited to aid in hunting and fishing 5. Plants and plant chemicals used medicinally and in rituals
	Symbolically-marked Groups	1. Convergent evolution of olfactory markers in social insects and arbitrary song dialects in birds and cetaceans 2. Apes and some monkeys engage in social learning of several behaviors, but do not use these for social categorization purposes 3. Elephants differentiate human scents, clothing and languages that map on to an ethnic boundary and respond to markers from only one of the groups as threats	1. Long-distance trade may have brought culturally different people into contact since Paleolithic 2. Mutli-ethnic empires and cities arise independently in several ancient civilizations (e.g., Mesopotamian, Egyptian, Roman, Inkan empires) 3. Evidence of ethnogenesis and ethnic mergers across history show boundaries are transient	1. Fetuses acquire linguistic information in utero, neonates can differentiate mother's language 2. Children interpret social group labels as suggestive of information richness 3. Early developing biases to prefer familiar dialect, and make predictions based on language use; no clear biases for use of visual markers 4. Social choices involving members of different groups often start around marriageable age	1. Symbolic markers universally used as cultural and coalitional identifiers 2. Groups marked by minor dialectical differences may act genocidally towards each other, while groups marked my large language differences can co-exist amicably 3. People belong to several hierarchically nested (e.g., lineages) and cross-cutting groups (e.g., age sets and religions)

3.1. *Cognitive design for learning about plants*

Plants are a fundamental part of human life. The archeological record and studies of modern hunter-gatherer and hunter-horticulturalist populations show that humans rely on plants in a variety of ways. Plants are a foundational component of human diets and the types of plant food resources typically exploited require intricate processing steps prior to consumption (e.g., Cordain et al., 2000; Crittenden and Schnorr, 2017; Kaplan et al., 2000). Plant consumption is a mode of subsistence with a deep evolutionary history, extending back through the hominin lineage (Harris and Hillman, 2014; Henry et al., 2014; Revedin et al., 2010; Ungar and Sponheimer, 2011). Of course, hominins are not unique in this respect. Plant consumption occurs across the animal kingdom and many intricate adaptations for plant consumption can be found in diverse species of insects, ungulates, monkeys, and apes, among many others (e.g., Knolhoff and Heckel, 2014; Palo and Robbins, 1991; Perry, 2011; Schuppli et al., 2016; van Schaik et al., 2003; Whiten, 2017; Whiten et al., 1999).

However, human use of plant resources is not limited to food. Modern hunter-gatherer and hunter-horticulturalist populations utilize plant material to manufacture artifacts (e.g., shelters, baskets, and a variety of other tools; Lee, 1993; Marlowe, 2010) and process plants to extract chemicals that are used in multiple ways, including as pigments for decoration, poisons for hunting and fishing, medicinal treatments, and psychoactive substances for ritual consumption (Begossi et al., 2002; Ringhofer, 2009; van Andel et al., 2013). There is evidence that prehistoric humans used plant fibers in rope and other materials as well (Hardy, 2008; Hardy and Kubiak-Martens, 2016).

Human interactions with plants are also not limited to adulthood. Younger infants are often carried along on foraging trips, and toddlers and young children often participate in food processing and preparation (e.g., Draper and Cashdan, 1988; Hewlett and Lamb, 2005). In some societies, children as young as 2–3 years of age engage directly in foraging activities, specializing in easy to obtain resources like fruits and berries (Bird and Bliege Bird, 2000; Boyette, 2016; Crittenden et al., 2009, 2013; Hawkes et al., 1995).

For all of the benefits humans can obtain from them, plants can also inflict serious costs. Plants have evolved a wide variety of toxic chemical compounds and physical defenses such as thorns and stinging hairs to protect themselves from damage caused by herbivores (Karban and Baldwin, 1997; Keeler and Tu, 1983; Palo and Robbins, 1991), some of which can be harmful or even fatal to humans. Further, plants are in coevolutionary relationships with many different herbivorous species, and most of these species possess very different physiologies and sensory systems than humans (e.g., insects, birds, etc.). Therefore, plants generally do not possess signals indicating that they are edible (or toxic) to humans. Some more general principles like aversions to bitter flavors can help guard against plant poisoning (e.g., Cashdan, 1994, 1998). However, a general aversion to bitterness is not sufficient on its own to construct a human diet or identify plants that might be useful in other ways. Many plant food items are bitter tasting, particularly prior to processing (e.g., cooking; Wrangham, 2009), and many bitter tasting plants possess useful chemical or physical properties that humans exploit.

These conditions suggest that, fundamentally, the adaptive problem humans face with respect to plants is to identify the beneficial plants in their local environment while avoiding the costs that dangerous plants can inflict (Wertz and Wynn, 2014a,b).

To be clear, a more fine-grained analysis of recurrent human-plant interactions suggests that there are actually several different adaptive problems humans face with respect to plants, and that, to some degree, these challenges overlap with other broader adaptive problems such as food learning and danger avoidance (e.g., Wertz and Wynn, 2014a; Włodarczyk et al., in press). However, this level of detail is beyond the scope of the current paper. For our current purposes, the more general form of the adaptive problem—avoiding plant costs while obtaining plant benefits—is sufficient to motivate the predicted design features discussed here.

The sections below explore three aspects of predicted cognitive design for human interactions with plants: (1) design for avoiding plant dangers such as poisoning and physical injury, (2) design for acquiring beneficial information about plant properties, and (3) design for generalizing learned information about plants. There are certainly other interesting aspects of cognitive design that are related to plant foraging, such as temporal and caloric return tracking (Smith and Winterhalder, 1992) and navigational and spatial skills (e.g., Krasnow et al., 2011; New et al., 2007). Although such design features are part of the full picture, for our purposes in this paper, we focus on the three aspects of predicted design highlighted here.

3.1.1. Avoiding plant dangers

There are two recurrent aspects of the environment that predict the possible design of plant danger avoidance mechanisms: (1) plants are rooted to the spot, and (2) plants do not reliably signal human-relevant dangers such as toxicity (e.g., Palo and Robbins, 1991). With respect to point (1), unlike other evolutionarily recurrent dangers such as snakes and spiders (Lobue and Deloache, 2011; LoBue et al., 2010; New and German, 2015) plants generally cannot move around on their own. Therefore, injury from plants occurs when a person moves themself physically close enough to a plant to make contact with it. Consequently, there is a simple way to decrease exposure to plant dangers, particularly in periods of vulnerability like infancy: minimize physical contact with plants. Further, point (2) suggests that the design of this behavioral avoidance strategy should be to initially avoid contact with all unknown plants, regardless of how they look. Based on this analysis, it was predicted that human infants would avoid touching plants (Wertz and Wynn, 2014b), regardless of whether the plants looked benign or were covered in sharp-looking thorns (Włodarczyk et al., in press).

To test this proposed design, 8- to 18-month-old infants were presented with plants and a series of control objects that matched the plants along different dimensions. Some of the control objects shared perceptual features of the plants (green color, presence of leaf-shaped parts), while others were also familiar to infants (small lamps, spoons, books), or were also naturally-occurring entities (stones and shells). As predicted infants were reluctant to touch the plants compared to all of the other stimulus types (Elsner and Wertz, under revised review; Wertz and Wynn, 2014b; Włodarczyk et al., in press; Włodarczyk et al., in preparation), and were just as reluctant to touch benign-looking plants as plants with thorns (Włodarczyk et al., in press). We have also collected data using a similar paradigm among the Shuar, hunter-horticulturalists living in the Ecuadorian Amazon who have extensive daily experience of and knowledge about plants. The preliminary results suggest that Shuar infants are also reluctant to touch plants compared to other types of entities (Wertz et al., in preparation).

These results support the predicted design of a behavioral avoidance strategy for plants in human infants. These predictions about design were made primarily considering sources of design typically emphasized by evolutionary psychologists. However, some initial evidence suggests infants may adjust their behavioral avoidance strategies contingent on social input from adults, particularly for their interactions with thorny plants (Włodarczyk et al., in press; Włodarczyk et al., in preparation). If these preliminary results hold, then future investigations would benefit from considering design that could arise from cultural systems such as teaching practices (e.g., Kline, 2015) or culturally-variable parent-child interaction norms (e.g., Mesman et al., 2016; Ochs and Schieffelin, 2001).

3.1.2. Learning about plant edibility

Next we turn to the predicted design of cognitive mechanisms to acquire beneficial information about plant properties. As outlined in Section 3.1, humans exploit plants for a variety of purposes including food resources, raw material for artifact construction, and sources of useful chemicals. Therefore, the scope of the information humans must acquire about plants is quite broad. However, we focus here specifically on design for acquiring information about plant edibility.

Here again there are important aspects of plants that suggest some critical design features: (1) all plants produce toxins, some of which can be harmful to humans but are not reliably signaled (Keeler and Tu, 1983), and (2) human diets are complex and many plant resources must be processed prior to consumption (e.g., Cordain et al., 2000; Kaplan et al., 2000). These conditions make trial-and-error learning about plants potentially very costly and suggest that learning about plant edibility is likely achieved via cognitive design for social learning (e.g., Boyd and Richerson, 1985; Feldman et al., 1996; Perreault et al., 2012).

Correspondingly, there is evidence that infants possess social learning mechanisms with design for selectively acquiring information about edible plants (Wertz and Wynn, 2014a). In these studies, 6- and 18-month-old infants watched an adult pluck a fruit from a plant and put it in his mouth, and then pluck a similar-looking fruit from a manmade artifact and put it in his mouth too. Despite seeing exactly the same social information demonstrated with both object types, infants selectively learned that the plant was edible. This finding can be interpreted as evidence for a prepared social learning mechanism (e.g., Barrett and Broesch, 2012) for learning about edible plants, or (equivalently) as evidence for a content bias (e.g., Henrich and McElreath, 2003) in the transmission of social information.

These results raise many questions about the scope of the proposed cognitive design. For example: are these selective social learning effects restricted to learning about plant edibility, or can they be applied more widely to other kinds of candidate food items? The latter option seems likely to be correct, but there is not yet empirical evidence that can cleanly distinguish between these proposals (although several studies are currently being conducted with infants to address such questions). In any case, such selective social learning procedures must operate along side other food learning mechanisms such as gustatory and olfactory cues to toxicity (e.g., avoiding bitter tastes: Birch, 1999; Garcia and Hankins, 1975; Hagen et al., 2013; Profet, 1992; although see Glendinning, 1994; Wang et al., 2004), conditioned taste aversions (Rozin, 1976), and food neophobia (Cashdan, 1994, 1998; Lafraire et al., 2016). Although the problem of food learning for humans is (of course) broader than learning about plant edibility, plants are undoubtedly a significant part of human food learning.

One of the more interesting aspects of learning about plant edibility is that many foraged plant resources are not edible until they are subjected to some degree of processing. The processing steps required can be quite complex. For example, acorns were a staple food source of the Chumash people of southern California from at least 5000 years ago until the early 20th century, despite their high concentration of bitter tannins (Timbrook, 2007). Timbrook describes acorn processing as follows: Acorns were first knocked from the trees, gathered from the ground, and spread on mats or placed in granaries (themselves made of a particular species of plant) to dry for 15–20 days. The acorns were next shelled and dried in the sun for another 10 days before being tossed in a winnowing basket to remove the brown skin that stuck to the outside of the seed. At this point, the acorns could be stored in baskets or processed further for consumption. Acorns were consumed in the form of a mush, which was prepared by grinding the acorns using a stone mortar and pestle and then sifting the flour. Next, the ground meal was leached with water in specially-made leaching basins to remove bitter tannic acid and cooked using boiling stones, which were heated in the fire and dropped into cooking baskets filled with acorn mush and cold water. The cooked mush was then scooped from the basket and eaten with roasted meat, seafood, or whatever else was on the menu.

Such complex processing techniques cannot be developed de novo by each individual. Rather these designs are the result of accumulated cultural information transmitted from one generation to the next. This kind of complex food processing is widespread across human societies–

similar cases have been documented for other staple plant foods such as maize, potatoes, and mongongo nuts (Johns, 1990; Katz et al., 1974; Lee, 1993). Further, there is evidence to suggest that culturally-transmitted dietary practices feed back onto natural selection. Human salivary amylase is an enzyme that breaks down starch, and human populations with higher starch diets possess more copies of a gene related to the expression of salivary amylase (AMY1) than populations with lower starch diets (Perry et al., 2007).

Taken together, these lines of evidence suggest that the cognitive mechanisms that support human food learning in general, including learning about plant edibility, are a rich area for generating and testing hypotheses about cognitive design. Critically, there is already suggestive evidence that such design reflects the entwined processes of natural selection and cultural evolution. Therefore, a full understanding of the cognitive mechanisms involved will require adopting the integrated framework we advocate.

3.1.3. Generalizing learned information to novel plants

We close this section with a discussion of the possible cognitive design for generalizing learned information about plants. This component of cognitive design is of fundamental importance for any kind of learned information. This is because, for learned information to be useful outside of the immediate context in which it is acquired, the cognitive architecture must systematically generalize the learned information to other entities in functional ways. For example, when a child learns the word "cat," in order to use that word appropriately in a communicative context, she must recognize the other entities in the world that are indeed cats and generalize the use of the learned word only to those entities (and not, for example, to dogs).

The principles underlying this kind of categorization and generalization have been studied extensively in the psychological literature (e.g., Bloom, 2000; Carey, 1985; Jones and Smith, 1993; Mandler and McDonough, 1998; Markman, 1989; Murphy, 2002; Rosch, 1999). Infants as young as 3 months of age categorize different types of animals and artifacts (see Rakison and Yermolayeva, 2010 for a review), including making rather fine-grained distinctions between types (e.g., between different species of domestic cats; Saffran et al., 2007). Categorization early in life is facilitated by social information and naming (e.g., Nazzi and Gopnik, 2001; Pauen et al., 2015; Träuble and Pauen, 2007), and there appear to be different categorization rules for different types of entities. For example, infants and young children tend to categorize artifacts by their shape (Landau et al., 1988; Mandler, 2000; Quinn and Eimas, 1996; Rakison and Butterworth, 1998), but seem to privilege color cues when categorizing food items (Addessi et al., 2005; Macario, 1991; Rioux et al., 2016). This literature suggests that infants and young children are quite adept at categorization and generalization, and that the rules they use to do this can be flexibly deployed across different types of content and situations. However, the generalization rules used for plants are not yet clear.

The problem of generalizing learned information about plants is quite complex. For example, consider the case of generalizing plant edibility. For many plants, only certain parts are edible while other parts of the same plant may be toxic. This is even the case for familiar domesticated plants (e.g., rhubarb and potato plants, which both have toxic leaves). Therefore, the generalization rules must not only pick out other plants of the same type, but the edibility inference must be narrowly applied *within* a plant. Conversely, if the learned information is that a certain type of grass is useful to making baskets, then that inference may be applied to the entire class of plants that share similar perceptual and material properties, even if they are not (botanically speaking) the same species of grass. This level of detail in generalization rules for plants has, to our knowledge, not yet been explored.

Nevertheless, there is some initial evidence that infants do systematically generalize learned information about plant edibility (Wertz and Wynn, under review), even though they fail to generalize learned edibility information about non-plant food items (Shutts et al., 2009). In these studies, 18-month-olds watched an actor eat fruits from one type of plant, and then were given the choice between two others: a plant that shared the same fruit color and leaf shape, and another plant that had a different fruit color and leaf shape. Infants chose to eat the fruits from the similar-looking plant. These results demonstrate that infants systematically generalize learned information about plant edibility. However, which features are used for this type of generalization (e.g., leaf shape, fruit color), and the specificity of the generalization (e.g., to the entire plant, or only to the other fruits) are not yet clear. Generalization of plant edibility has also been shown in other species. For example, sheep show systematic generalization of edibility based on plant species type, but not plant height (Edwards et al., 1997; Ginane and Dumont, 2006), while bumblebees generalize based on flower color (Dukas and Waser, 1994).

There is good reason to suspect that, similar to the learning rules discussed in Section 3.1.2, generalization rules for plants may also be subject to cultural evolution. Folkbiological taxonomies—the informal rules that are used to categorize plants and animals—differ systematically across cultures. For example, the folkbiological taxonomies of children and adults living in traditional societies tend to have more specificity than those of children and adults living in industrialized towns and cities (Anggoro et al., 2008; Coley, 2000; Coley et al., 1999; Lopez et al., 1997; Medin and Atran, 1999). Any hypotheses based on the form of explicitly held plant knowledge in traditional societies may, however, be difficult to test on a broad scale as this kind of knowledge is rapidly disappearing from the world as the subsistence practices of such societies change with increasing market integration (e.g., Kuhnlein and Turner, 1991; Reyes-Garcia et al., 2005).

3.1.4. Summary

The available empirical evidence suggests that the entwined processes of natural selection and cultural evolution play a significant role in the predicted aspects of cognitive design for learning about plants. This work suggests that the cognitive design includes features for (1) avoiding plant harm by minimizing physical contact with plants, (2) selectively learning about plant edibility, and (3) appropriately generalizing learned information. The ideas outlined above lend themselves to further hypothesis development and empirical testing to elucidate the design of plant learning systems in the human mind.

3.2. Cognitive design for learning about symbolic groups

In all modern human societies culturally-acquired symbolic or linguistic features demarcate socially meaningful differences between groups of people. The subset of these features that serve signaling functions are often called ethnic markers when they map onto regional cultural areas, foci of identity, or cooperative units. While such markers are omnipresent in human societies in the ethnographic, historical, and archaeological records (Moffett, 2013), their evolutionary depth is less clear. Paleolithic humans used ochre and shell beads as far back as 100,000 years ago, but the symbolic function of these tools and their associations to other cultural traits is ambiguous (D'Errico et al., 2005; Henshilwood et al., 2011). On the earlier end of the hominin lineage, it is unlikely that our common ancestors with chimpanzees did anything approximating the use of such ethnic markers given that not much cultural content is associated with residential groups in most apes, and the cultural traits that differ between groups do not seem to serve signaling functions (Whiten et. al. 1999). In fact, recent analyses suggest that cultural traits in chimpanzee societies may trace matrilines more than residential group boundaries (Wrangham et al., 2016). Furthermore, virtually no other vertebrate species uses culturally-evolved markers to identify unknown individuals as group members (Moffett, 2013).

Another person's group membership, as determined by these arbitrary linguistic or symbolic markers, has many important consequences for social interactions. These markers can help adults decide whether to avoid each other, trade with each other, marry each other, steal from each other, or murder each other (Cashdan, 2001; Levine and Campbell, 1971). These marker-based interaction decisions can function either (1) because the markers indicate that individuals have other cultural features that are relevant for the interaction, or (2) because other people moralize interactions across certain group boundaries. As an example of the first kind of incentive, consider that humans have been engaging in long-distance trade since the Paleolithic (McBrearty and Brooks, 2000). This suggests that one early selective pressure for culturally-evolving signalling systems was to efficiently communicate to others which resources they could offer, or which exchange norms they would follow (e.g., norms about how hard to bargain; Bunce and McElreath, 2017; McElreath et al., 2003). This would allow individuals to capitalize on the gains in trade from interacting across culturally different groups (Moya and Boyd, 2015; Pisor and Gurven, 2016). As an example of the latter incentive—i.e., group-based moral prescriptions—the ethnographic record demonstrates a wide range of marriage systems that can either prescribe that one should marry others who speak the same (Sharda, 1990), or different (Jackson, 1983), languages. In such cases, making the appropriate marital choice may be rewarded by other people, while marrying a socially unacceptable person may come with punishment or ostracism. This means that appropriate behavior towards members of different groups can provide reputational benefits.

One of the challenges for an individual learning to navigate an ethnically marked world, is that similar symbolic and linguistic markers can also be used to signal within population differences including status, kin group, coalitional membership, gender, or age sets (Milroy and Milroy, 1993). Not only are the groups that markers map onto diverse, but so is the information observers can reap from the symbols, the information the user intends to signal, and the forms that these symbolic markers take (e.g., tattoos, dialects, clothing choices or phonemic, lexical, syntactic differences). This means that humans must solve several adaptive challenges including, (1) identifying which kinds of traits serve group marking purposes, and are not just idiosyncratically variable, (2) determining what are the best ways to interact with individuals from a given group, and (3) generalizing this information—i.e., who else counts as having the same trait, and which other characteristics are associated with that group membership. These three tasks are somewhat analogous to the challenges related to learning about plants described above: determining what counts as a (potentially dangerous) plant, learning whether a plant is edible, and generalizing this learned information. While the adaptive challenges are not completely overlapping, we will focus our discussion on the functionally similar tasks.

3.2.1. Identifying group markers

There are several possible mechanisms that could allow humans to first identify traits that serve group marking purposes. Natural selection could have favored useful Bayesian priors regarding which cues would be informative (e.g., a prior that speech vocalizations will be more informative than other sounds). Alternatively, natural selection could have favored expectations that social groups would exist in the world, but maintain a more open parameter that required direct cultural input to determine how groups were delineated. Furthermore, it is possible that the symbolically marked worlds humans created change natural selection on these algorithms.

The comparative animal cognition literature gives us clues about possible sources of design for identifying symbolic group markers. Several species have evolved to attend to conspecific dialectical differences, often for territorial purposes (Kershenbaum et al., 2012; Rendell and Whitehead, 2001; Salinas-Melgoza and Wright, 2012). However, with the possible exception of some whale societies (Cantor and Whitehead, 2015), in most non-humans it is unlikely that dialectical differences carry much information about the cultural features of group members. Cultural markers thus play a more limited role in intergroup interactions in most species than they do in humans (Robinson and Barker, 2017).

Some species that do not produce group markers themselves nonetheless use the cultural information conveyed by human linguistic and symbolic cues to predict patterns of human behavior. For example, elephants have been shown to act more aggressively towards Maasai-typical garments than Kamba-typical garments, and more defensively when hearing Maasai male voices than Kamba male voices–adaptive responses given that Maasai men are more likely than Kamba men to hunt elephants (Bates et al., 2007; McComb et al., 2014). This research suggests that a selective history of culturally-marked conspecifics is not necessary for at least some species to learn to make functional use of the information available in human ethnic markers over the course of their development. Although it remains unclear what aspects of cognition might be shared across elephants and humans to enable such inferences, it is possible that cognitive mechanisms that genetically evolved for reasoning about predators (McComb et al., 2011) or other species boundaries (Gil-White, 2001) may play a role in learning about symbolically marked groups. However, neither the existing research on humans nor that on non-humans fully specifies the cognitive mechanisms that allow them to use information about ethnic markers.

This non-human literature does not exclude the possibility that humans have specific adaptations for detecting symbolic group boundaries. Among the traits humans use as symbolic group markers we have the best evidence that linguistic differences are a common and automatic bases of categorizing others (Cohen, 2012; Labov, 1972; Nettle and Dunbar, 1997). Some work with American adults suggests that, like gender, and unlike race (Kurzban et al., 2001; Pietraszewski et al., 2014; Pietraszewski, 2018), dialect differences are encoded and used to remember what a person said, even when a cross-cutting coalitional or visual cue is provided (Pietraszewski and Schwartz, 2014a,b; Rakic et al., 2011). However, this research cannot distinguish at least two different accounts of why people consistently categorize others along gender and linguistic boundaries. First such a biased expectation could have been genetically specified as Bayesian priors because these boundaries recurred as important social classifiers for much of our evolutionary history. Alternatively, the gender and dialectical differences used in the study could have been ones that culturally-evolved to be important indicators of non-coalitional information and people use learning mechanisms that evolved for detecting other kinds of associations to figure this out. Were the latter account accurate, several questions would still need to be addressed including; what these learning mechanisms look like and why certain linguistic boundaries culturally evolved to be socially meaningful even if they are not coalitional.

The fact that language acquisition is an important adaptive task for infants may make it easier for linguistic markers to acquire social meaning in societies. We know that the capacities for discriminating between languages start developing in humans when they are fetuses. Neonates are capable of differentiating their mother's language from foreign languages with different cadences based on audio inputs they receive in utero (Nazzi et al., 1998), and by 5 months of age they can differentiate some regional accents of the same language (Cristia et al., 2014). This capacity probably initially genetically evolved in fetuses and infants for language acquisition purposes since learning to speak and understand speech is likely important earlier in development than is choosing interaction partners. This does not mean that language boundary recognition does not require social inputs. On the contrary, the developing child must learn which linguistic features matter for differentiating accents (Floccia et al., 2009). Furthermore, this capacity does not necessarily mean that infants or neonates treat linguistic cues as group markers. We return to the question of how infants use linguistic information for social purposes later.

It is clear that in many cultural contexts non-linguistic symbolic markers (e.g., sartorial or religious markers) will be most important for delineating social boundaries and children must be capable of learning these alternative social taxonomies (Hirschfeld, 1998; Moya and Boyd, 2015, 2016). As an illustration of this developmental diversification, while young children show a mild bias towards reasoning as if social identities were genetically inherited, these kinds of beliefs diversify through adulthood according to cultural context and the features of the social boundary (Moya, 2017). For learning these diverse social taxonomies it seems that children have cognitive mechanisms specifically designed for learning about social categories based on labels provided as verbal cues. Heyman and Gelman (2000) show that 3- to 4-year-old American children will predict that humans who have the same novel labels applied to them will share other traits (e.g., novel preferences, personality traits, and skills), but will not make such predictions when the novel labels are applied to the same pictures and these are described as dolls. Generic labels referring to multiple, rather than specific individuals, are also more important than visual cues of similarity in promoting memory for racial categories (Hirschfeld, 1993). Similarly, we have found no evidence that body morphology is a privileged means of categorizing strangers despite its visual accessibility (Moya and Boyd, 2016). On the other hand, other visual cues like sartorial styles (Moya and Boyd, 2016), or intentional markings (Brase, 2001) might be weighted more heavily early in development as a plausibly important group marker. This suggests the possibility that, as with ethnolinguistic boundaries, culturally structured worlds with stylistically marked boundaries favored genetic selection for psychological priors that these cues would be important bases of social delineation.

3.2.2. *Determining how to interact with others of a given group*

Once a developing child learns the locally-relevant symbols delineating groups in their environments, they face a second adaptive challenge of using others' group membership to choose how to interact with them. These algorithms would need to facilitate learning about correlations between symbolic markers, interaction-relevant traits, and prescribed social interactions. A similar set of possible adaptations could be at play for this task. For example, humans might have genetically-evolved priors to avoid, or learn more about, others who are identified as not belonging to the same symbolically marked category. Furthermore, certain ways of talking about symbolically marked groups could have culturally evolved to help children acquire useful social taxonomies and intergroup interaction norms.

We see some evidence that infants and children preferentially use linguistic cues for social purposes. By 10 months of age infants preferentially accept toys from strangers who speak their parents' same dialect (Kinzler et al., 2007) and by 14 months they preferentially imitate actions of native language speakers (Buttelmann et al., 2013). Similarly, young children preferentially choose friends who speak the same dialect over same-race friends even in contexts with important histories of racism (Kinzler et al., 2009), and treat language-use as if it were a genetically inherited trait, even in places where adults do not (Gelman and Hirschfeld, 1999; Moya et al., 2015). These pieces of evidence minimally suggest that humans have genetically evolved prior expectations that linguistic cues will have social meaning. Again, this expectation will require social inputs to develop and refine according to the local environment (Cohen and Haun, 2013; Pietraszewski and Schwartz, 2014b). This privileging of linguistic information for social purposes might also be bootstrapped from genetically evolved mechanisms for language acquisition in various ways. For example, language discrimination capacities can serve as inputs either for other genetically-evolved social group specific mechanisms, or broader social learning mechanisms that also acquire complex culturally-evolved social taxonomies.

Clearly group-based interaction norms develop around non-linguistic symbolic boundaries as well, for example in the case of religious boundaries. By middle childhood children start acquiring this knowledge through social learning. Generic labels that promote social categorization also promote more essentialist beliefs (i.e., that identities are innate and informative) in American children and adults (Rhodes et al., 2012). Randomly assigned group labels, and to a lesser extent shirt colors, also foster ingroup favoring resource allocations, and implicit and explicit attitudes among American children (Dunham et al., 2011). Infants, on the other hand, only show preferences for others with the same food preferences or color mittens under specific circumstances–i.e. when these cues are not arbitrarily assigned and the other puppet exhibits a dissimilar preference after the infant has made their choice (Hamlin et al., 2013; Mahajan and Wynn, 2012). This result suggests that infants' behavior on the task may reflect more interpersonal assessments of others who choose to behave similarly or dissimilarly to oneself. The later development of ingroup favoring behavior towards arbitrary groups, and the ethnographic diversity of intergroup interaction norms (Levine and Campbell, 1971) suggests that most information about how to treat members of different symbolic groups has to be socially acquired.

The fact that children easily socially learn which markers denote meaningful boundaries, and how to treat those with and without those markers allows cultural evolutionary processes to play an important role in the design of group stereotypes and intergroup norms. For example, ideologies that encourage immigration, and discourage emigration may well be favored by such processes (Bell and Moya, 2018.; Moya and Scelza, 2015). Social Identity Theorists' have amassed much evidence that people favor ingroups, and care about their groups' reputation (Tajfel, 1982), but lack a cogent evolutionary explanation of the phenomenon. One possible explanation for ingroup favoritism is that positive beliefs about one's group culturally evolved because they persisted over ideologies that suggested one's group was subpar. Positive ingroup ideologies could have encouraged group-beneficial behaviors if properly incentivized within the group (e.g., people who are not patriotic enough are scorned), while ingroup denigrating beliefs may well have encouraged emigration (Boyd and Richerson, 2009). This is counter to the typical psychological enterprise of trying to provide an individual motivation for such group-based self-esteem. Similarly, norms about who can become a group member, including essentialist beliefs, have important demographic implications and therefore consequences for the persistence of beliefs and group boundaries (Moya, 2017). How such beliefs are maintained in the face of conflicting information, or even when it does not behoove individuals to believe such propaganda is an open question, but several models suggest punishment and reputational awards can help stabilize otherwise costly beliefs and behaviors (Boyd and Richerson, 1992; Suzuki and Akiyama, 2005). This enterprise of understanding the kinds of boundaries that are likely to culturally evolve, and the design features they might have is an underdeveloped research enterprise in the social sciences.

3.2.3. *Generalizing learned information to novel individuals*

Finally, information that one learns about different groups and how to treat them must be generalized to the right set of individuals. How similar does a stranger's symbolic marker have to be to that of a known individual for one to infer that they have a shared feature and generalize across it? About which novel features can one safely generalize? Again one might posit various genetic algorithms and cultural rules that could help solve this problem. While we do not have complete answers to any of these questions, the empirical literature reveals that a mosaic of pre-cultural cognitive adaptations, hominin-specific genetic adaptations, and cultural technologies are likely brought to bear on these adaptive challenges.

Again, linguistic cues and verbal labels play a role in guiding inductive inferences. Before age 8 children in highland Peru expect speakers of the same language to share similar novel preferences and social networks, even though adults in this context do not (Moya, 2013). Furthermore, among American children the same information conveyed in the form of verbal labels promotes more predictions about peoples' preferences, beliefs, and activity patterns than if it is provided as descriptions of behavior (e.g., X is a carrot-eater vs. X eats carrots; Gelman and Heyman, 1999). How these strategies of generalization reflect genetic and cultural designs is ambiguous, though given the vast array of stereotypes that culturally evolve, it is likely that most of the traits people associate with specific group boundaries must be socially acquired.

3.2.4. Summary

There is strong evidence that humans are well designed to use symbolic group marker information to categorize others, and decide on how to interact with them. The suit of adaptations involved likely include learning algorithms shared with non-cultural species, language acquisition cognition that makes us attuned to fine grain linguistic distinctions early in our development and ascribe them social meaning, and label-based social learning that facilitates the adoption of culturally-evolved social taxonomies. Once learned, these social taxonomies serve as well-designed cognitive schemes for navigating complex social worlds.

4. Conclusion

The disciplinary boundaries within the evolutionary social sciences investigating the mind roughly correspond to research traditions that focus more on natural selection and those that focus more on cultural evolution. We have attempted to demonstrate how evolutionary psychology and cultural evolution can find common ground through the study of design. Through this lens, the approaches of these two research traditions can complement each other, and provide a framework for developing a wider range of testable hypotheses about cognitive design. We hope this recognition of different pathways to design will broaden the hypothesis space in the evolutionary social sciences and encourage methodological pluralism in the investigation of the mind.

Acknowledgements

The authors were funded by the Max Planck Society while writing this manuscript. We would like to thank P. Richerson, D. Pietraszewski, B. Barrett, K. Panchanathan, M. Gervais, the EEHBC lab group at UC Davis, and an anonymous reviewer for their feedback on previous versions of this manuscript.

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