Behavioural Processes 161 (2019) 87–93

Contents lists available at ScienceDirect

Behavioural Processes

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

Selected emergence in the evolution of behavior and cognition

H. Clark Barrett

Department of Anthropology, UCLA, Los Angeles, CA, 90095-1553, United States

ARTICLE INFO

Keywords:
Evolution
Ontogeny
Phenomics
Gene-culture coevolution
Selected emergence

ABSTRACT

In the evolution of cognition and behavior, a recurrent question concerns the degree to which any given aspect of the phenotype has been "selected for" or "specified," as opposed to arising as a byproduct of some other process. In some sense this is the key question for evolutionary theories of development that seek to connect ultimate evolutionary accounts to proximate developmental accounts of ontogeny. A popular solution to the specification problem is to invoke "emergence," in which phenotypes are co-constructed by many causes and cannot be reduced to any one of them. However, the concept of emergence, while appealing, can obscure sources of ultimate causation by leaving them unspecified. Here I explore the idea of selected emergence, in which phenotypic outcomes do emerge from a confluence of factors, some haphazard, but which include in part a history of selection, genetic and / or cultural, to produce phenotypic outcomes of that type. I discuss potential case studies of selected emergence, explore its empirical implications and provide suggestions for future research on the evolution of emergent outcomes.

1. Introduction

Among the most notorious of unnatural human experiments are cases of children who grow up in environments without language. These horrible cases of deprivation and trauma demonstrate unambiguously not only that language is learned, but that a specific kind of environment is necessary for humans to acquire it. The fact that most humans do learn languages that vary in innumerable ways, under an enormous variety of conditions, suggests that the human capacity to learn human languages is developmentally robust and reflects something about human biology. While our close evolutionary relatives the great apes can learn some aspects of human languages when raised by humans, data from ape language studies strongly suggest that human languages, as used by human children and adults, are only fully learnable by members of our species. In other words, there is something about both human languages and humans themselves–including the nature of human sociality and the nature of human biology–that enable us to develop into linguistic beings. This is a classic example of a developmental interaction, in which an organism's phenotype is co-caused by its biology (including but not limited to its genetic endowment) and the environment in which it develops.

This much is well known and relatively uncontroversial (though there is controversy about just how much and what aspects of human languages great apes can acquire). However, it is a curious fact about the state of the behavioral sciences that despite widespread agreement about the importance of interactions in development–and certainly in the development of cognition and behavior, including language–our set of conceptual and technical tools for thinking about and studying those interactions remains strikingly impoverished. Nearly everyone rejects the simple binaries implied by the nature/nurture distinction, such as ideas of "pre-specification" of phenotypic outcomes, or purely blank-slate learning (e.g., Karmiloff-Smith, 2009). A popular alternative is the idea of emergence: phenotypic outcomes emerge developmentally through an interaction of genomic and environmental factors (Bates et al., 1998; Elman et al., 1996; MacWhinney, 2006; Quartz & Sejnowski, 1997). While this is a useful concept, it can sometimes be used in ways that obscure rather than clarify the roles that evolutionary processes have played in producing phenotypic outcomes. In this paper I explore the potential usefulness of a novel concept, *selected emergence,* for thinking about the contributions of different processes, including genetic evolution, cultural evolution, and chance, to the construction of phenotypes.

To introduce this concept I will begin with language phenotypes as potential examples of selected emergence. However, the concept of selected emergence applies broadly to any aspect of the phenotype that emerges through the conjunction of natural selection and other causal factors. Therefore, language is but one of the many phenotypic phenomena to which the concept of selected emergence applies. First, I will explain the concept and how it contrasts with non-selected or by-product emergence. I will then explore several phenotypic domains of behavior and cognition where it may usefully apply including language, artifacts, and social norms.

E-mail address: barrett@anthro.ucla.edu.

https://doi.org/10.1016/j.beproc.2018.04.019
Received 3 September 2017; Received in revised form 5 March 2018; Accepted 24 April 2018
Available online 04 May 2018

2. The concept of emergence

In the philosophical literature there is a debate about how the term "emergence" should be properly used, but a useful gloss is as follows: "emergent entities (properties or substances) 'arise' out of more fundamental entities and yet are 'novel' or 'irreducible' with respect to them. (For example, it is sometimes said that consciousness is an emergent property of the brain.)" (O'Connor and Wong, 2015, p. 1; see Clayton & Davies, 2008; Meehl & Sellars, 1956; Kim, 2006; Schaffner, 1998). Emergence can thus be contrasted with reduction, which is one reason it is a popular concept among those who reject the nature/nurture dichotomy.

In the developmental literature, the concept of emergence is sometimes used to imply that a phenotypic outcome is caused by multiple factors, including genetic influences on development, without being "pre-specified" (Karmiloff-Smith, 2009). In other words, emergent phenotypic outcomes are byproducts or "coincidences," in the sense of being co-caused by a combination of factors that led to the outcome without that outcome being selected for or targeted by a developmental system. For example, consider this passage from Elman (2005):

It is clear that something about human biology is essential to learning language (despite impressive demonstrations of non-human primates' communication skills, no non-human comes anywhere close to mastering human language). A crucial question then is what it is that is species-specific – is it also domain-specific, specialized knowledge that subserves only language? And is it the ability for symbol processing? Or does language emerge as a consequence of multiple phenotypic modifications that are not in themselves specific to language but which collectively make language possible? (Elman, 2005, p. 112).

Here, an emergentist account of language is contrasted with a selectionist account, or a "selection for" account, of language. In the selectionist / selection for account, the ability to learn language has been specifically selected for and is, therefore, an adaptation. In the emergentist account, on the other hand, the ability to learn language is a byproduct of selection for other things which make possible or enable the acquisition of language without linguistic abilities specifically having been selected for. As Elman puts it, the emergentist view is that "language sits at the crossroads of a number (how many – a dozen? thirty?) of small phenotypic changes in our species that interact uniquely to yield language as the outcome… Here, language is seen as a domain-specific outcome that emerges through the interaction of multiple constraints, none of which is specific to language" (Elman, 2005, p 113). The phrase "none of which is specific to language," here, points out the contrast between selectionist / selection-for accounts and non-selectionist or *byproduct* emergence accounts. Because, according to Elman's conjecture, language is enabled by evolutionary changes that are not specific to language—i.e., they have not been selected *because* they enabled language skills in the past—then this account yields language as a byproduct, potentially of selection for other, non-language related phenotypes, or even because of drift. This differs from a selected emergence account in which language does emerge through a confluence of causal factors, some of which are not specific to language, but at least some of which are evolutionary changes that were favored by selection because they produced language phenotypes that increased fitness.

In principle, both byproduct emergence and selected emergence accounts of phenotypic phenomena such as language are theoretically plausible. There are many accounts of language both as adaptation (Pinker & Bloom, 1990), and as byproduct or epiphenomenon (Christiansen & Chater, 2008). It is certainly possible that some or all of human capacities to acquire language are epiphenomena, byproducts, exaptations, or spandrels, in Gould's (1991) sense. Indeed, the language-as-spandrel idea is popular in the language evolution literature (Hauser et al., 2002; Piatelli-Palmarini 1989). However, more evolutionary scenarios exist than pure byproduct emergence on the one hand and on the other, as Elman puts it, "domain-specific, specialized knowledge that subserves only language." For many in this literature, there seems to be an idea that the stronger selection is, the more precise phenotypic specification will be, but that is not necessarily the case. It is possible for selection to favor phenotypic outcomes without those outcomes being strongly specified by developmental systems (Oyama et al., 2001). Instead, complex phenotypes such as language phenotypes may be products of natural selection acting on emergent processes of development, such that these emergent processes tend to produce language phenotypes under certain conditions (e.g., in children raised in language environments) without those outcomes being precisely specified by the developmental system, and without highly detailed "innate knowledge." This is the idea behind selected emergence (Barrett, 2015).

3. Selected emergence

Selected emergence can be contrasted with byproduct emergence in that aspects of selected emergent outcomes may reliably recur across generations and individuals *because* these aspects have been selected for, while other aspects of the developed phenotype are haphazard, variable across individuals, and not directly the result of a history of selection for them. From a selected emergence perspective, phenotypes ("outcomes") cannot be carved into units that can then be sorted as wholes into discrete categories such as "adaptations" and "byproducts." Instead, selected emergent outcomes are examples of true emergence in which one kind of causal factor, natural selection acting over evolutionary time, interacts with other causal factors orthogonal to selection to produce the outcomes. These can include factors such as genetic drift, cultural evolution, historical contingencies and local conditions. The result is a phenotypic whole that has some features or aspects that are the products of selection, but others that are not. The phenotypic manifold of an organism will have adaptive functional properties as well as many arbitrary, neutral, variable, and possibly even maladaptive features, and these can be mixed inseparably in the same "trait" or "phenotype". This is, in fact, a general feature of phenotypes that are the product of natural selection, because selection is always just one among many causal processes shaping them. Developed language phenotypes are good examples of mixes of functional features (e.g., features that enable effective communication) and non-functional junk. Importantly, even many "arbitrary" features, such as the fact that the word "cow" in English refers to cows, are at the same time functional–they allow speakers to communicate effectively about cows–and, in some sense, arbitrary historical accidents, in that other sound-meaning pairs would be equally effective.

Again, language here is being used as just one potential example of a phenotypic product of selected emergence (for more on language as a specific case, and for examples in addition to language, see below). In the case of language, we might consider the sum total of an individual's developed language abilities to constitute his or her language phenotype. Much or most of her language phenotype is an idiosyncratic product of her particular historical developmental context, including many features unique to that individual. Her language phenotype is in this sense an emergent product of many factors, most of which are causally independent of, indeed random with respect to, any history of natural selection acting on language capacities. But this does not necessarily imply that selection played no role in shaping aspects, possibly quite important aspects, of the emergent outcome. Indeed, one would imagine that most aspects of cognition and behavior in most organisms are both emergent and enabled by selection in some way. The important evolutionary questions are: first, *what* aspects of a given emergent phenotype have been shaped by selection and the myriad of other causal processes acting at different levels and scales, and second, *how,* in terms of process? Elman's question, i.e., whether selection has acted on language phenotypes *per se* over evolutionary time, is indeed one of the most important questions to ask, and is in a sense *the*

important question regarding the (possible) adapted / selected nature of human language capacities. But the fact that language phenotypes emerge from multiple causal processes, which is necessarily true, is not sufficient to answer the question.

In some ways selected emergence is not a new idea, given that most or perhaps all developed phenotypes emerge as a consequence of multiple causal factors including but not limited to natural selection. Of what use is it then? Its potential usefulness lies in the potential not only to replace monocausal theories of development, but also to allow for more causal possibilities than are typically afforded by traditional ways of thinking about nature and nurture. An analogy, here, might be to niche construction theory (Odling-Smee et al., 2003). Niche construction is a phenomenon that presumably happens most or all of the time, given that organisms often modify their environments in ways that have consequences for their own future evolution. Niche construction theory could thus be accused of having the flaw of being too general, or too vague. But this overlooks the fact that niche construction, like natural selection, is a phenomenon that takes many forms. Thus, a proper theory of niche construction requires delving into the details, creating taxonomies, models of different kinds of niche construction processes, etc. Similarly, selected emergence is probably ubiquitous, because even aspects of the phenotype that can be properly considered adaptations comprise a mix of features that have been selected for and features that have not. However, the value of the selected emergence concept is that it allows us to get past the hopeless task of carving phenotypes into discrete adaptations versus byproducts to see how the phenotypic whole is a mix of features that arise from a history of selection and features that are neutral or arbitrary with respect to histories of selection.

4. Phenotypic types and tokens

If the account sketched above is right, then many if not most aspects of organismal phenotypes will be the result of selected emergence at some level. For any given part of the phenotype that interests us, then, the question will be: what is the actual mix of causal processes that accounts for the evolution and development of this phenotypic trait? As Elman points out in the case of language phenotypes, there is clearly a range of possibilities that vary in the specificity or granularity of how selection has acted on the developmental system (for a discussion of the granularity of domains see Atkinson and Wheeler, 2004). One way of conceptualizing this granularity is in terms of phenotypic types and phenotypic tokens (Barrett, 2015). To take the case of the English word "cow," most would agree that this word (and its neural and embodied instantiation in the brains of English speakers) is a phenotypic token, a token of a language phenotype. But a way of rephrasing Elman's question is, what is the evolutionary *type,* or degree of granularity, of which this token is an exemplar? Supposing for the moment that natural selection has in *some* way played a role in the ability to acquire the lexical item "cow," there are many possibilities for just what that role has been. For example, has natural selection specifically acted on the ability to learn word-meaning mappings, such that "cow" is a token of the evolutionary type *word*? Or has natural selection acted on the ability to form sensory-meaning mappings more generally, such as the smell of cakes to cakes, such that "cow" is a token of the evolutionary type *association*? Or perhaps "cow" is the emergent result of an even more general ability, such as "learning," so that the type of which "cow" is a token is *learned item*? These are only a few of a small number of possibilities, each of which is an example of selected emergence, but where *what* has been selected for varies.

The use of formulations like "selected for" is contentious, for good reason, so it is worth unpacking what it means in this case. The evolutionary process (including selection, drift, etc.) is historical, and acts only on variants that appear. This means that natural selection never acts on anything as abstract or general as "language," "symbols," or "associations," but only on actual phenotypes, including specific states of the organism at every stage of development. Thus, natural selection only acts on tokens—in other words, actual, developed phenotypes–never on types, or the set of all *possible* phenotypes that could be produced by a given developmental process. By analogy, in the biological literature on adaptive plasticity and reaction norms, theoretical models show that natural selection can favor plastic developmental systems—as used here, a kind of type—but only via selection on specific phenotypic outcomes, never on the trait of plasticity itself *except* to the extent that it (the type) is expressed in actual phenotypes (tokens) (Via et al., 1995).

What use is it, then, to speak of types? One reason is practical: virtually all constructs in the social and behavioral sciences are formulated in terms of types. For example, "learning," “plasticity,” "groups," "norms," "biases," "memory," "categorization," etc. are all types of processes or phenomena that only ever occur as tokens. No organism forms "categories" in general, only specific ones. Thus, an evolutionary or developmental account that refers to any of these as having been "selected for" suffers from the same problem of referring to abstractions that lump together individual tokens conceptually. But this is a general feature of science–we need terms to refer to things in terms of shared properties–and so is not in itself fatal. More important is that type accounts that vary in granularity also vary in what causal processes they posit to have occurred (two accounts *don't* vary in this way are essentially the same account). To say that word-meaning mappings are a type that has been selected for is, more or less, to say that word-meaning mappings are phenotypes that have occurred in the past and varied in a way that impacted fitness, *and* that they played some causal role in the history of selection that differs from other "types", such as other instances of sensory-meaning associations. How that role differed is at the crux of the specificity question.

The account of selected emergence proposed here is consistent with other accounts that treat development of phenotypes as co-caused by many factors, and where selection plays a causal role in shaping developmental resources such that some phenotypes reliably emerge but only given the availability of other causal factors. For example, in Millikan’s etiological account of functions, a token trait of an organism, such as a lexical item (“cow”), has a function, such as the function of referring to cows, if some ancestor token of the same type (e.g., words, lexical items) was selected for because of that function in the past (Millikan, 1984). This makes that function the “proper” function of the phenotypic token—consistent with the view proposed here and similar views in the literature on evolution and functions (e.g., Barrett, 2015; Sperber, 1996; Tooby and Cosmides et al., 1992). The selected emergence view is also consistent with developmental systems perspectives that view phenotypic development as co-caused and appeal to dynamics within causal networks rather than “pre-specification” or “innateness” to explain how selection can produce phenotypes that develop reliably through emergence (Griffiths & Gray, 1994; Oyama et al., 2001). It also fits nicely with the Greenough et al.’s (1987) concept of “experience-expectant” development, in that selected emergence relies on the presence of certain causal factors that were present during the history of selection in order to produce developmental tokens that possess type-level adaptive properties that were selected for in past tokens. Moreover, according to this account, selection can shape organisms to seek out certain kinds of experiences which can then shape emergent phenotypic outcomes. In all of these accounts, phenotypes are produced through interactions between multiple factors; thus, selected emergence is an “interactionist” developmental perspective that allows a history of selection to be part of the causal network that explains phenotypic outcomes, without *reducing* the cause of adaptive phenotypic outcomes to selection alone (Pearl, 2009).

Selected emergence, then, refers to selection as just one causal component acting within the complex causal networks that shape organismic design. The evolutionary developmental (evo-devo) literature asks how natural selection can shape developmental outcomes within these complex causal webs, taking into account factors like pleiotropy

and developmental modularity (Raff, 1996, 2000; Wagner & Altenberg, 1996). An important set of questions concerns how selected emergence acts within the constraints imposed by developmental networks in a given case: for example, to what degree can selected emergence target certain “modular” aspects of the phenotype, as opposed to influencing multiple phenotypic outcomes through pleiotropy (Wagner and Altenberg, 1996)? This will be a largely empirical question depending on the details of the case, so we will not discuss it in detail here. However, the selected emergence view fits well with a “hierarchical modularity” model of mind and brain in which modularity occurs at multiple levels of the architecture and emerges through developmental processes that produce modularity (functional specificity) in the phenotype via ontogenetic processes of feedback between internal systems and the external environment (Barrett, 2015). Selection can, metaphorically speaking, tweak the knobs of developmental systems to produce different kinds of functional outcomes within hierarchically modular systems.

5. Signatures of selected emergence

Using the terminology of types and tokens, selected emergence occurs when an emergent phenotype is a token of a type that positively impacted fitness in the past, even though the specific phenotypic token is an emergent combination of many immediate particulars and historical contingencies (Barrett, 2015; Millikan, 1984). Here, with some grammatical apologies, I will call such phenotypes “selectedly emergent.” Importantly, the culturally evolved environment can play a huge role in shaping the emergent outcomes of development, and often in ways that are not entirely coincidental or haphazard with respect to histories of selection. Indeed, in cases of culture-gene coevolution, both the cultural and genetic forms of natural selection contribute to selectedly emergent outcomes, because culturally transmitted environments and information become part of the "normal" or "typical" environment in which development occurs (Boyd & Richerson, 1985). For example, in the case of language it's quite likely that culturally transmitted languages have evolved in tandem with genetic changes that together enable the acquisition of language (Christiansen & Chater, 2008; Christiansen & Kirby, 2003; Deacon, 1998; Fisher, 2017). Learning "cow," then, is in some sense an emergent accident of the child experiencing speech acts involving "cow" in her developmental environment, but is also likely an example of selected emergence because the genetically transmitted resources that enabled her learning spread in humans because they enabled us to learn words. This is a plausible, indeed likely, evolutionary hypothesis, but how can we evaluate it empirically?

Testing evolutionary hypotheses is notoriously difficult, but not impossible–especially if one's goal is to use data to narrow down hypothesis space, pruning away some alternatives and raising the posterior probability of others. Usefully, there are some empirical signatures that we might expect to be associated often, but not always, with selectedly emergent outcomes.

First, because we are talking about products of natural selection (including both genetic and cultural versions), we expect selectedly emergent outcomes to exhibit hypothesis-relevant functionality, at least under a certain range of conditions. Second, however, we expect to see variation even in functional properties, for several reasons. One, of course, is that there is always variation even in fitness-proximal traits (Houle, 1991). Another is that even when selection has favored certain kinds of emergent phenotypic properties, the causal contributors to those emergent outcomes may vary across environments or individuals. For example, it has been proposed that culture-gene coevolution has favored humans' ability to engage in large-scale cooperation to a degree not seen in closely related primate species (Richerson & Boyd, 2005). This requires both genetically and culturally evolved ingredients: a genetically evolved propensity to acquire to and adhere to social norms that promote sociality, along with social norms that are the products of historical competition between sets of norms, resulting in cultural evolution towards norm complexes that progressively stabilize larger groups. These ingredients combine to produce selectedly emergent social outcomes in the form of functioning societies composed of many individuals who have acquired and adhere to social norms to varying degrees. Thus, we expect stable large-scale social configurations to arise via selected emergence, but there may be substantial variation across individuals and social groups even in functional, fitness-relevant features such as individual success in the society. We expect this variation to exist despite the fact that it may be the target of genetic and cultural selection, precisely because selection is acting on, but has not eliminated, fitness-relevant variation in the emergent outcomes.

Third, for many cases of selected emergence we expect to see dimensions of neutral or near-neutral variation within the envelope of selectedly emergent phenotypic outcomes. This is because many developed phenotypic tokens may successfully play the same causal role. This is sometimes known in evolutionary theory as *functional equivalence* (Hubbell, 2005). For example, selection might have acted to enable the acquisition of word-meaning mappings, where those specific mappings are local conventions that evolve via processes of linguistic evolution. If so, then the individual tokens of word-meaning pairs that are present in the language phenotypes of individual speakers will be highly variable around the world, and that variation–for example, whether cows are referred to with the English word "cow" or the French word "vache"–will be neutral or near-neutral in terms of fitness. The same goes for other products of selected emergence discussed below, such as artifacts and social norms: the ability to acquire and use them may be due to selection, but there may nevertheless be substantial, near-neutral variation in individual phenotypic details, such as whether a greeting involves a handshake or a kiss on the cheek. Of course, for reasons described above, there may well be non-neutral, fitness-relevant variation in these selectedly emergent outcomes as well: for example, one tool may be more efficient than another for cutting down trees, even though both are selectedly emergent aspects of the extended phenotypes of their users. In other words, products of selected emergence may have many dimensions of spandrel-like, neutral variation that participates in their function but that could be substituted for another variant, e.g., "vache" for "cow," without a loss of function, similarly to how functionally equivalent variants of a gene can be substituted for each other (Greer et al., 2000). This is potentially related to the concept of “equifinality” in the developmental literature, in which there can be multiple pathways to a given end state within an open system (Cicchetti & Rogosch, 1996). If the end state in question is, for example, a functioning lexicon—seemingly a selectedly emergent feature of all languages—then there are many possible lexicons that are equivalently or near-equivalently functional, assuming multiple language speakers share them (cultural population dynamics, therefore, play a role in their emergence and stabilization).

An implication of this idea of functional equivalence and near neutrality is that variants may be exchanged or substituted across individuals or groups, and sometimes removed entirely, without loss of function. For example, successful linguistic communication typically makes use of devices such as grammatical rules and word-meaning mappings, but there are many other routes to transmission of meaning, including pragmatics. What one language does with a grammatical rule another may do with context or other linguistic devices. Languages might vary, then, in things like size of the lexicon or morphological complexity, without proportional variation in linguistic expressivity. If language phenotypes were genetically "specified" one might not expect the same substitutability (Evans & Levinson, 2009).

Finally, when we look at the details of cases of selected emergence, we may see that some causal components that contribute to selectedly emergent outcomes may appear "impoverished" or "underspecified" with respect to the outcome, because they only provide part of what is necessary to produce the outcome in question. For example, it may well be that some genetic variants have swept to fixation or near-fixation in

humans because they enable spoken / gestural language–for example, lineage-specific variants in the *FOXP2* gene–though the proximate functional effects of these genes do not appear to be restricted to language per se (Enard et al., 2002; Graham & Fisher, 2015). To test hypotheses about why these genetic changes have occurred, it is important to formulate hypotheses in terms of all the causal complements required to produce the hypothesized emergent outcomes, e.g., the culturally transmitted complement, and to test the hypotheses accordingly.

These are but a few of the empirical signatures that one might expect in cases of selected emergence. The details will depend on the nature of the hypothesized interactions between genes and environmental and cultural factors. Importantly, however, there are many more theoretical alternatives that the binary possibilities of byproduct emergence versus genetic specification, and it is in the fleshing out of these alternatives and their predicted empirical signatures that progress can be made.

6. Some examples

Selected emergence may be expected in cases where some genetic change or changes in the human lineage have enabled new behavioral skills, but where cultural evolution, niche construction, or other extra-genetic processes have given rise, in combination with the genetic changes, to new phenotypes whose fitness benefits stabilize those changes. Here languages, artifacts, and social norms are briefly considered as possible examples of selectedly emergent outcomes.

6.1. Languages

As noted above, languages have long been a focal point for the nature-nurture debate. Accounts of language evolution range from highly nativist, strongly implicating natural selection acting on genetic resources for language (Friederici & Chomsky, 2017; Pinker & Bloom, 1990), to highly empiricist, strongly implicating learning (Elman et al., 1996; Christiansen and Chater, 2008; Evans and Levinson, 2009). More nativist accounts tend to posit language as a self-contained, “modular” system (e.g., Chomsky’s account of a Language Acquisition Device; Chomsky, 1986), though some accounts, such as Pinker and Bloom’s (1990), allow for a much more flexible architecture. Accounts also vary in the degree to which they posit language as the specific target of natural selection, as opposed to language arising as a byproduct of selection favoring other, perhaps more general-purpose changes (Anderson, 2010; Deacon, 1998; Elman, 2005).

Despite these debates, several facts about languages and their evolution are undisputed. First, languages must clearly be learned and are culturally transmitted. Second, humans appear to be the only species that can learn them, suggesting some genomic contribution to language phenotypes (whether that contribution comes from genes selected because of their effects on language phenotypes, or as a byproduct of selection for something else, or even genetic drift). Languages exhibit all of the empirical signatures mentioned above: they are functional yet exhibit substantial variation, much of it presumably neutral or nearly so, within that functionality. We do not yet have anything close to the full story of what uniquely derived genomic changes in our lineage enable language acquisition, use, and transmission, though there are some intriguing candidates including autapomorphies in the *FOXP2* gene, some of which swept to near-fixation prior to the split between humans, Neanderthals, and Denisovans, and a more recently discovered regulatory change that appears to have been subject to a selective sweep approximately 50,000 years ago (Enard et al., 2002; Krause et al., 2007; Maricic et al., 2012).

Whatever genomic changes might have enabled language in humans, these changes are clearly not sufficient by themselves to produce linguistic phenotypes. Language is not in this sense "innate," but rather, emerges in development through exposure to a linguistic social environment. In fact, though it is difficult to quantify, one might argue that most of the information in linguistic knowledge comes from the social environment, and therefore, that most linguistic knowledge is not in any way "specified" in the human developmental program. However, this does not mean that languages exist or are transmitted purely as emergent byproducts of selection for something else, or of no selection at all. Instead, it seems plausible if not likely that the communicative and representational advantages afforded by language have long had substantial fitness benefits to humans. If so, then these benefits likely contributed to the selective advantages stabilizing the derived genetic changes that make language possible, qualifying the emergence of language skills during development as a case of selected emergence.

Importantly, individual "languages" or linguistic tokens (words, rules) cannot be considered to be products of genetic selection specifically for those tokens. This is an important sense in which individual language phenotypes can be said to be emergent products of a genome that has (perhaps) been under selection to enable language phenotypes as a type, along with culturally transmitted information, subject to processes of cultural evolution, that produce individual language phenotypes as emergent outcomes. Importantly, even the cultural evolutionary processes that shape individual language are a mix of selection and drift, i.e., historical change among functionally equivalent or near-neutral variants.

6.2. Artifacts

Human-made artifacts, such as tools, clothing, buildings, information storage technologies and the like may also provide good examples of selectedly emergent phenotypic outcomes. In some sense tools and the knowledge and skills surrounding them may be said to be part of the human extended phenotype (Dawkins, 2016). They are prosthetics that can influence the fitness of their users, so genomic or other biological changes that enable their creation, use, and transmission, as well as their environmental effects, can be subject to selection, similarly to genes enabling language (Odling-Smee et al., 2003).

For artifacts as for languages, key questions concern the granularity or specificity of outcomes, i.e., types, that have been selected for over evolutionary time. There is no question that specific phenotypes related to artifacts, such as the ability to use a pencil or a tennis racket, are emergent products of some genomic changes in the human lineage that make acquisition of such skills possible, combined with idiosyncratic local information, including information gleaned from both social and individual learning.

An often-noted conundrum is that many artifacts are clearly evolutionarily novel, leading to the question: how can our ability to use them be the product of selection? Here again, the concept of selected emergence can help to resolve this conundrum. Some genomic changes, leading to changes in, e.g., patterns of cortical and sub-cortical wiring during development, may have been selectively favored precisely because they enabled the manufacture and use of more sophisticated artifacts in the human lineage. Selection could have favored, for example, the ability to develop more fine-grained motor skills and the combination of multiple steps in producing and using artifacts such as tools (Johnson-Frey, 2004). There is evidence that the dorsal visual stream is particularly well-suited to processing information about artifacts, possibly due to selection to do so (Kravitz et al., 2011). These changes may be critical to our ability to use artifacts like pencils and tennis rackets today, even though these are clearly evolutionarily novel and culturally idiosyncratic artifact tokens. Because of this novelty and parochiality, the idea of emergence–as opposed to, e.g., innateness– is necessary to explain their acquisition. This is suggested by theories of "neuronal recycling" or "neural reuse" that are invoked to explain why dedicated brain areas can develop for evolutionarily novel skills like reading and writing (Anderson, 2010; Dehaene and Cohen, 2007; Geary, 1995). Crucially, stable aspects of the environment, including highly evolved cultural practices, may be required for these “novel” aspects of the

phenotype to develop, such as dedicated areas for visual processing of words in the brain (Dehaene and Cohen, 2007). Nevertheless, even in cases of evolutionary novelty such as word form areas in the cortex, these might not pure byproducts, since word form areas reliably develop in areas of cortex dedicated to object processing more generally, and it is possible that words and writing systems have co-evolved with human object recognition mechanisms in a way that makes writing systems easily legible and processable by our brains (Dehaene, 2009; Morin, 2015). Cultural practices such as writing and reading, and learning of certain forms of knowledge through school (e.g., formal mathematics), may serve as useful case studies for selected emergence, because we can compare phenotypes across individuals with and without the relevant experience.

6.3. Social norms

Some Americans greet others by shaking their hands, and willingly eat chicken eggs before noon but not after. Like the pairing of the sound "cow" with cows, these behaviors seem as arbitrary and idiosyncratic as one could imagine, and few would suggest that they are directly the products of natural selection. However, they may be good examples of selected emergence, if natural selection has favored genomic changes in the human lineage that enable learning of and adherence to social norms (Chudek and Henrich, 2011; Richerson and Boyd, 2005). As in the case of languages and artifacts, individual tokens of social norms may be evolutionarily novel and thus never, by themselves, contributed to selection on aspects of the genome that make their acquisition possible. Instead, social norms evolve culturally in individual populations over generations, so that the particular set of cultural norms, representations, and behaviors that characterize an individual are the products of selected emergence.

An interesting feature of selected emergence is that once it is enabled by a combination of genomic and cultural evolutionary changes, new evolutionary and population dynamics may occur as a result. This can be seen as a kind of population-level, historical form of emergence. For example, social norms and practices are well-known to “feed back” on themselves, influencing the conditions of their own spread, stability, or demise. Moreover, mixes of social conditions can produce new emergent phenomena, such as the selfie, or oscillating fashion cycles (Bourdieu, 1984). No theorist would dream of attributing these directly to natural selection, but they may not be pure byproducts either. For example, the culture of selfies might be an expected consequence of human social psychology. In these cases, histories of selection might contribute elements such as motivations, desires, or patterns of response to social reinforcement (e.g., being socially admired, increasing the size of one’s network), while evolutionarily novel technologies such as photos and the internet may act as amplifiers or prostheses for those motivations. These cases seem like good examples of selected emergence.

7. Conclusion: open questions

If a concept such as selected emergence is to be of any use, it must offer insights and the potential for progress beyond the conceptual tools already available to biologists and social scientists. The primary virtues of the selected emergence concept are its ability to replace nature/nurture formulations such as "specification" and to provide precise causal parsing of cases in which the genomic contribution to development appears insufficient by itself to account for observed phenotypes, and yet where those phenotypes are nevertheless products, at least in part, of a history of selection. Still, to be of use the concept will require substantial fleshing out, and many open questions remain.

Perhaps the most important question in any given case of selected emergence will be how to properly describe the granularity of phenotypic outcomes that have contributed to selection in the past. For example, in the case of human-specific autapomorphies in the *FOXP2* gene, there remains an important open question regarding to what degree language phenotypes contributed to the selective sweeps of these variants (Graham & Fisher, 2015). Various sources of evidence can contribute to narrowing down hypothesis space, including inferences about the timing of the sweeps–for example, whether they predate or post-date the split of our lineage from that of Neanderthals and Denisovans–and archaeological evidence concerning the behavioral repertoires of these taxa at the time of the sweeps (Krause et al., 2007; Dediu & Levinson, 2013). Moreover, data on phenotypic effects of genetic variance at this locus in contemporary people, along with data on effects of variation in *FOXP2* homologs in other taxa, tell us something about the functional consequences of the gene (Fisher, 2017; Graham & Fisher, 2015). From such data we know that *FOXP2* plays a role in coordinating motor activity and plays a role in cortico-basal ganglia circuits influencing the dopaminergic system of the striatum (Enard et al., 2009; Haesler et al., 2007). Based on this, it is possible that human-specific *FOXP2* variants were selected because of benefits in some kind of motor activity unrelated to language, such as manufacture and use of complex tools. Or, these variants might have been favored specifically because they enabled motor skills of speech and gesture—or some combination of both. Progress will be made through explicitly laying out the theoretical alternatives and their empirical implications, and, importantly, in recognizing that genomic changes are just one (potentially small) part of the causal complement necessary to produce selectedly emergent phenotypes such as tool-use skills or language.

Many sources of evidence, some potentially counterintuitive, may help to narrow down hypotheses concerning cases of selected emergence in humans. These can include phylogenetic inferences regarding the evolution of genomic components of selectedly emergent outcomes, but also phenotypic inferences derived from studies of genomic variation in present-day humans, as well as studies of functional consequences of homologs in other species. Increased understanding of the genome and epigenome in humans and other species, along with finer-grained descriptions of the human cognitive and behavioral phenome, gleaned from, e.g., brain mapping, developmental and cross-cultural behavioral studies, will help us to understand how genes and gene regulation interact with social and physical environments to produce emergent phenotypic outcomes, and how these can be linked to histories of selection in the past.

References

Anderson, M.L., 2010. Neural reuse: a fundamental organizational principle of the brain. Behav. Brain Sci. 33 (4), 245–266.

Atkinson, A.P., Wheeler, M., 2004. The grain of domains: the evolutionary-psychological case against domain-general cognition. Mind Lang. 19 (2), 147–176.

Barrett, H.C., 2015. The Shape of Thought: How Mental Adaptations Evolve. Oxford University Press, Oxford.

Bates, E., Elman, J., Johnson, M., Karmiloff-Smith, A., Parisi, D., Plunkett, K., 1998. Innateness and emergentism. In: Bechtel, William, Graham, George (Eds.), A Companion to Cognitive Science. Basil Blackwell, Oxford, pp. 590–601.

Bourdieu, P., 1984. Distinction: A Social Critique of the Judgement of Taste. Harvard university press.

Boyd, R., Richerson, P., 1985. Culture and the Evolutionary Process. University of Chicago Press.

Chomsky, N., 1986. Knowledge of Language: Its Nature, Origin, and Use. Greenwood Publishing Group.

Christiansen, M.H., Chater, N., 2008. Language as shaped by the brain. Behav. Brain Sci. 31 (5), 489–509.

Christiansen, M.H., Kirby, S., 2003. Language evolution: consensus and controversies. Trends Cogn. Sci. 7 (7), 300–307.

Chudek, M., Henrich, J., 2011. Culture–gene coevolution, norm-psychology and the emergence of human prosociality. Trends Cogn. Sci. 15 (5), 218–226.

Cicchetti, D., Rogosch, F.A., 1996. Equifinality and multifinality in developmental psychopathology. Dev. Psychopathol. 8, 597–600.

Clayton, P., Davies, P. (Eds.), 2008. The Re-Emergence of Emergence: The Emergentist HypoThesis from Science to Religion. Oxford University Press.

Dawkins, R., 2016. The Extended Phenotype: The Long Reach of the Gene. Oxford University Press.

Deacon, T.W., 1998. The Symbolic Species: The Co-Evolution of Language and the Brain. WW Norton & Company.

Dediu, D., Levinson, S.C., 2013. On the antiquity of language: the reinterpretation of neandertal linguistic capacities and its consequences. Front. Psychol. 4.

Dehaene, S., 2009. Reading in the Brain: The New Science of How We Read. Penguin.
Dehaene, S., Cohen, L., 2007. Cultural recycling of cortical maps. Neuron 56 (2), 384–398.
Elman, J.L., 2005. Connectionist models of cognitive development: where next? Trends Cogn. Sci. 9 (3), 111–117.
Elman, J.L., Bates, E.A., Johnson, M.H., Smith, A.K., Parisi, D., Plunkett, K., 1996. Rethinking Innateness: A Connectionist Perspective on Development. MIT Press, Cambridge, MA.
Enard, W., Gehre, S., Hammerschmidt, K., Hölter, S.M., Blass, T., Somel, M., Brückner, M.K., Schreiweis, C., Winter, C., Sohr, R., Becker, L., 2009. A humanized version of *FOXP2* affects cortico-basal ganglia circuits in mice. Cell 137 (5), 961–971.
Enard, W., Przeworski, M., Fisher, S.E., Lai, C.S., 2002. Molecular evolution of *FOXP2*, a gene involved in speech and language. Nature 418 (6900), 869.
Evans, N., Levinson, S.C., 2009. The myth of language universals: language diversity and its importance for cognitive science. Behav. Brain Sci. 32 (5), 429–448.
Fisher, S.E., 2017. Evolution of language: lessons from the genome. Psychon. Bull. Rev. 24 (1), 34–40.
Friederici, A.D., Chomsky, N., 2017. Language in Our Brain: The Origins of a Uniquely Human Capacity. MIT Press.
Geary, D.C., 1995. Reflections of evolution and culture in children's cognition: implications for mathematical development and instruction. Am. Psychol. 50 (1), 24.
Gould, S.J., 1991. Exaptation: a crucial tool for an evolutionary psychology. J. Soc. Issues 47 (3), 43–65.
Graham, S.A., Fisher, S.E., 2015. Understanding language from a genomic perspective. Annu. Rev. Genet. 49, 131–160.
Greenough, W.T., Black, J.E., Wallace, C.S., 1987. Experience and brain development. Child Dev. 58 (3), 539–559.
Greer, J.M., Puetz, J., Thomas, K.R., Capecchi, M.R., 2000. Maintenance of functional equivalence during paralogous *hox* gene evolution. Nature 403 (6770), 661–665.
Griffiths, P.E., Gray, R.D., 1994. Developmental systems and evolutionary explanation. J. Philos. 91 (6), 277–304.
Haesler, S., Rochefort, C., Georgi, B., Licznerski, P., Osten, P., Scharff, C., 2007. Incomplete and inaccurate vocal imitation after knockdown of *FOXP2* in songbird basal ganglia nucleus Area x. PLoS Biol. 5, e321. http://dx.doi.org/10.1371/journal.pbio.0050321.
Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: what is it, who has it, and how did it evolve? Science 298 (5598), 1569–1579.
Houle, D., 1991. Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution 45 (3), 630–648.
Hubbell, S.P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Funct. Ecol. 19 (1), 166–172.
Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. Trends Cogn. Sci. 8 (2), 71–78.
Karmiloff-Smith, A., 2009. Nativism versus neuroconstructivism: rethinking the study of developmental disorders. Dev. Psychol. 45 (1), 56.
Kim, J., 2006. Emergence: core ideas and issues. Synthese 151 (3), 347–354.
Krause, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R.E., Burbano, H.A., Hublin, J.J., Hänni, C., Fortea, J., De La Rasilla, M., Bertranpetit, J., 2007. The derived *FOXP2* variant of modern humans was shared with neandertals. Curr. Biol. 17 (21), 1908–1912.
Kravitz, D.J., Saleem, K.S., Baker, C.I., Mishkin, M., 2011. A new neural framework for visuospatial processing. Nat. Rev. Neurosci. 12 (4), 217.
MacWhinney, B., 2006. Emergentism—use often and with care. Appl. Linguist. 27 (4), 729–740.
Maricic, T., Günther, V., Georgiev, O., Gehre, S., Ćurlin, M., Schreiweis, C., Naumann, R., Burbano, H.A., Meyer, M., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Gajovic, S., Kelso, J., Enard, W., Schaffner, W., Pääbo, S., 2012. A recent evolutionary change affects a regulatory element in the human *FOXP2* gene. Mol. Biol. Evol. 30 (4), 844–852.
Meehl, P.E., Sellars, W., 1956. The concept of emergence. Minn. Stud. Philos. Sci. 1, 239–252.
Millikan, R.G., 1984. Language, Thought, and Other Biological Categories. MIT Press, Cambridge, MA.
Morin, O., 2015. How Traditions Live and Die. Oxford University Press.
O'Connor, Timothy, Wong, Hing Y.u, 2015. Emergent properties. In: Edward, N., Zalta (Eds.), The Stanford Encyclopedia of Philosophy, (Summer 2015 Edition)URL =. http://plato.stanford.edu/archives/sum2015/entries/properties-emergent/.
Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. Niche Construction: the Neglected Process in Evolution. Princeton University Press.
Oyama, S., Griffiths, P.E., Gray, R.D. (Eds.), 2001. Cycles of Contingency: DeveLopmental Systems and Evolution. MIT Press, Cambridge, MA.
Pearl, J., 2009. Causality: Models, Reasoning, and Inference, 2nd edition. Cambridge University Press, Cambridge.
Piatelli-Palmarini, M., 1989. Evolution, selection and cognition: from "learning" to parameter setting in biology and in the study of language. Cognition 31 (1), 1–44.
Pinker, S., Bloom, P., 1990. Natural language and natural selection. Behav. Brain Sci. 13 (4), 707–727.
Quartz, S.R., Sejnowski, T.J., 1997. The neural basis of cognitive development: a constructivist manifesto. Behav. Brain Sci. 20 (4), 537–556.
Raff, R.A., 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. University of Chicago Press, Chicago, IL.
Raff, R.A., 2000. Evo-devo: the evolution of a new discipline. Nat. Rev. Genet. 1 (1), 74–79.
Richerson, P., Boyd, R., 2005. Not by Genes Alone: How Culture Transformed Human Evolution. University of Chicago Press.
Schaffner, K.F., 1998. Genes, behavior, and developmental emergentism: one process, indivisible? Philos. Sci. 65 (2), 209–252.
Sperber, D., 1996. Explaining Culture: A Naturalistic Approach. Blackwell, Malden, MA.
Tooby, J., Cosmides, L., 1992. The psychological foundations of culture. In: Barkow, J., Cosmides, L., Tooby, J. (Eds.), The Adapted Mind: Evolutionary Psychology and the Generation of Culture. Oxford University Press, New York, NY, pp. 19–136.
Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Schlichting, C.D., Van Tienderen, P.H., 1995. Adaptive phenotypic plasticity: consensus and controversy. Trends Ecol. Evol. 10 (5), 212–217.
Wagner, G.P., Altenberg, L., 1996. Complex adaptations and the evolution of evolvability. Evolution 50 (3), 967–976.