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Evolutionary Biology and the Strategic View of Ontogeny: Genetic Strategies Provide Robustness and Flexibility in the Life Course

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It is difficult to synthesize evolutionary and developmental approaches to morphology, physiology, and behavior. Here we sketch one way to achieve such a synthesis that invokes ideas from evolutionary game theory. Developmental trajectories are often sensitive to environmental conditions. We reject the view, which is popular with some, that this sensitivity is well explained by a general plasticity. Instead we argue that flexibility is founded on a genetically encoded strategy, most or all of which is shared by the members of a population. Flexibility in the life course is achieved by the conditionalities inherent in the strategy. The strategy, which evolved by natural selection, allows an effective response to environmental variability. This enables organisms to perform well under a broad range of circumstances—a property that engineers call *robustness*.

One of the earliest and most influential attempts to integrate evolution and ontogeny was made by Haeckel (1874) who argued in his recapitulation theory (or biogenetic law) that essentially all phenotypic differences among species arise late during development. His clever idea was that species can evolve only by the terminal addition of new adult stages at the end of ancestral developmental sequences. He believed, for example, that all vertebrates went through nearly identical developmental stages until very late in the developmental process. A chicken embryo and a human embryo would be almost impossible to distinguish—at least if one is examining Haeckel's famous drawings. Unfortunately for Haeckel, his ideas were stronger than the facts. Sedgwick (1894) was one of the first to contest

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Haeckel's claims. He argued that even closely related species can be distinguished throughout development. And, indeed, it is now widely recognized that there are often dramatic differences between species in early development. A chicken egg, for example, is many thousand times larger than a human egg, and the latter does not have a hard shell. Even more impressively, although most frog species have a tadpole stage, some do not.

Despite the rejection of Haeckel's views for early development, his ideas have lived on in modern biology in the notion of a conserved phylotypic stage. Whatever differences exist early in development, there seems to be an intermediate phase in which embryos in broad ranges of taxa closely resemble each other. Genetic studies have also identified highly conserved patterns of genes and gene expression. The Hox cluster of genes is a well-known example (e.g., McGinnis & Krumlauf, 1992). Perhaps evolution can easily act on early stages because there are only a few relatively independent developmental modules: Modifying one module would not interfere with the processes in other modules. But evolution can less easily act on intermediate stages because these stages consist of larger numbers of mutually dependent modules: Changing one would interfere with the processes of many of the others (R. A. Raff, 1996). Yet even this view is now being called into question (E. C. Raff & R. A. Raff, 2000). Richardson et al. (1997) contended, for example, that evolution has produced a number of changes in supposedly conserved embryonic stages of vertebrates, including differences in body plan, numbers of repeating units, patterns of growth, and timing in development.

The debate on the ability of evolution to modify all stages of development, which has ranged from Haeckel's time to our own, touches on the problem of robustness and flexibility in the evolution of the life courses of different species. This debate can be extended to differences in the ontogeny of individuals within a single species. Here the conventional view would be that an individual's life course can be described as a unilineal sequence of species-typical ontogenetic stages—the life cycle. But there can be massive differences between individuals in the life course. Sexual differentiation is an obvious example. Even within a sex phenotypic ontogenies can strongly diverge. In two taxonomic families of fig wasps, for example, there exists a striking dimorphism in males. Hamilton (1979) described a species in which some male wasps are winged with small mandibles and others are wingless with huge mandibles that allow them to chop male competitors into pieces. Another well-known example of within-sex differentiation is that of worker and queen in a colony of social insects, such as bees. The differentiation does not stop here. Some species of ants produce workers who develop into living food containers, called honeypots. Other worker ants feed nectar to the honeypots who soon become unable to walk and simply hang from the ceiling of a "storeroom." The honeypots regurgitate the stored nectar back to workers when food is needed.

How can such dramatic differences in development, not only between but also within species and within the sexes of a single species, be understood? We know that feeding a developing bee royal jelly is enough to cause a female bee to become a reproductive individual instead of a neuter worker. Many biologists and psychologists would think that this answers the question and shows that an environmental difference (the presence or absence of royal jelly) is the source of developmental divergence. Is there no role for genes?

We now present a framework for understanding the evolution of this ontogenetic flexibility as the product of robust, genetically encoded strategies.

A STRATEGIC VIEW OF DEVELOPMENT

Although it may seem counterintuitive, we along with many other biologists believe that game theory, originally developed to explain strategic behavior in human interactions, can illuminate the evolution of physiological and morphological development in living organisms. The justification for this strategic view follows from obvious and not so obvious insights. An obvious insight is that Darwin's theory of natural selection assumes individuals compete for limited resources to reproduce and that selection tends to improve their competitive abilities. Game theory was invented to analyze what the best strategies would be in competitive situations when there is a conflict of interest. For example, is there a best strategy for playing a board game, such as chess or checkers? Here is how game theorists have approached this question. They first worry about what can be assumed about the other players. The conventional assumption is that all players are rational and everybody knows that everybody knows that everybody is rational. If this assumption holds, then game-theorists would try to identify so-called *Nash equilibria*. A Nash equilibrium is a combination of strategies, one for each player, such that each of these strategies is a best response to the others: Each player's strategy yields the highest payoff for her or him, given the strategies of the other players. It is called an equilibrium because under these conditions no player has an incentive to deviate from her or his strategy. To get a feel for the game-theoretic notion of a *strategy*, it is useful to consider the game of chess. Roughly speaking, a strategy is a list of instructions telling the player how to move in every single situation that may arise during the game. The reader can easily see that in practice it would often be difficult or nearly impossible for an individual to analyze a game and discover its Nash equilibria.

It is not obvious how a theory that depends on complete rationality of all players, each of whom must determine what to do in every situation that might arise, could apply to animals and plants. Surprisingly, this is possible if one considers that natural selection can provide individuals with their strategies instead of letting them choose the strategies themselves (Hammerstein, 2001; Maynard Smith, 1982). In this case, the trial-and-error process of natural selection, not the player herself or himself, "learns" how to play a Nash equilibrium (or an evolutionarily stable strategy as biologists would call it; there are some subtle differences between these concepts that we do not consider here). An interesting implication of this perspective is that evolutionary game theory is not confined to behavior because natural selection (not the brain) does the strategic analysis. An example of an evolutionary game that applies to morphology, not behavior, answers a question many of us have asked: Why are trees tall? Here is one reason derived from the strategic perspective. Suppose all trees were short plants in need of sunlight. If individual plants had no conflict of interest, they would be best off by remaining relatively short and not wasting resources on unnecessary growth, thereby maximizing the number of seeds they could produce. As soon as a single mutant plant gets taller than its neighbors, however, it can overshadow them, consuming some of their sunlight. The mutant would produce more seeds relative to its competitors and have somewhat more descendants. After many generations, all plants would be taller. Interestingly, if plants had brains they could individually analyze their competitive situation and decide to become taller. We would walk through the same forest. Natural selection thus evolves phenotypes that share many aspects with strategies derived from rational strategic analysis of conflict.

IMPLICATIONS OF THE STRATEGIC VIEW

The analogy between natural selection and strategic analysis helps us understand important issues in the evolution of development and ontogenies. We begin with the question of why many traits, such as the heart and the lung, develop very reliably in all members of a given species. The answer is that evolution has adapted a species to a particular ecological niche, providing it with all the basic equipment needed to survive and reproduce in this environment. Just as it would be difficult if not impossible to play ice hockey without skates or feet to put them on, it would be difficult for a lion to reproduce without teeth and claws. Most approaches to development have focused on how this “standard equipment” comes into being. Although the strategic view incorporates these approaches, it also dramatically extends them. As the tree example shows, phenotypes are expressions of a strategy, but strategies can be far more complex than simply growing to a particular height. Because a strategy is a list of actions to take in different circumstances and because phenotypes can be expressions of a strategy, the strategic view implies that individuals within a species will not necessarily develop along the same path. Just like moves in a game depend on the state of play, development should be sensitive to particular environmental conditions, taking one path in some circumstances and another path in other circumstances.

A well studied example is that of water fleas (*Daphnia*). Sometimes a water flea population experiences high levels of predation, and sometimes it is low. In principle water fleas are capable of developing a helmet-like morphological structure that protects them from predators (Brooks, 1965). The helmet is not free, however, because resources need to be allocated to its construction that could be used for reproduction instead. A strategic view would suggest that water fleas should build the helmet only when they need it. This argument only makes sense, of course, if water fleas can sense the presence of predators far in advance of an attack. It turns out that *Daphnia* predators leave chemical traces—kairomones—in the water that *Daphnia* can detect. In experiments, the relative helmet length of *Daphnia* almost doubles in the presence of caged predators (Agrawal, Laforsch, & Tollrian, 1999). The development of the helmet is thus conditional on a perceived cue that indicates that one developmental "move" would be better than another. Like a good chess player, water fleas make the right move. The data show that when predators are present, *Daphnia* with helmets experience dramatically lower mortality from predation. See Figure 1.

Water fleas are not the only organisms with conditional development of defenses. Even plants can develop strategically. When wild radish plants are eaten by a particular caterpillar, the plants produce tenfold higher concentrations of mustard oil, a chemical defense, on newly formed leaves. Although the plants cannot avoid the initial attack, they deter subsequent feeding by the caterpillars and other herbivores (Agrawal, 1999). More examples of what biologists call *inducible defenses* can be found in Tollrian and Harvell (1999).

THE ROLE OF THE GENOME

If a developmental psychologist or a behavioral geneticist had studied the helmets of water fleas, they would probably have convinced themselves rather quickly that the phenotypic variation in helmets is mainly caused by environmental variation. Indeed, this has been shown to be correct: Genetically identical water flea clones develop a wide range of helmet sizes that correlate very strongly with environmental conditions. One might be tempted to conclude that genes play a small role, if any. If so, where did the strategy of varying helmet size come from? Why are the helmets, when they do develop, so similar in structure? And is it just an accident that they work so well? Unlike humans who learn to make their helmets from others with more experience, water fleas do not learn how to make their helmets from anyone. They do not have the cognitive means to strategically analyze the threat from predators and design effective armor.

Natural selection, however, does have the means to analyze the threat and design an appropriate response. Natural selection produces functional organismic traits by conducting large numbers of experiments over hundreds or thousands of generations. Each of the randomly arising mutations sets up a new experiment. The success or failure of this experiment over many generations manifests itself in the chemical structure of the genome. Natural selection is, therefore, commonly con-

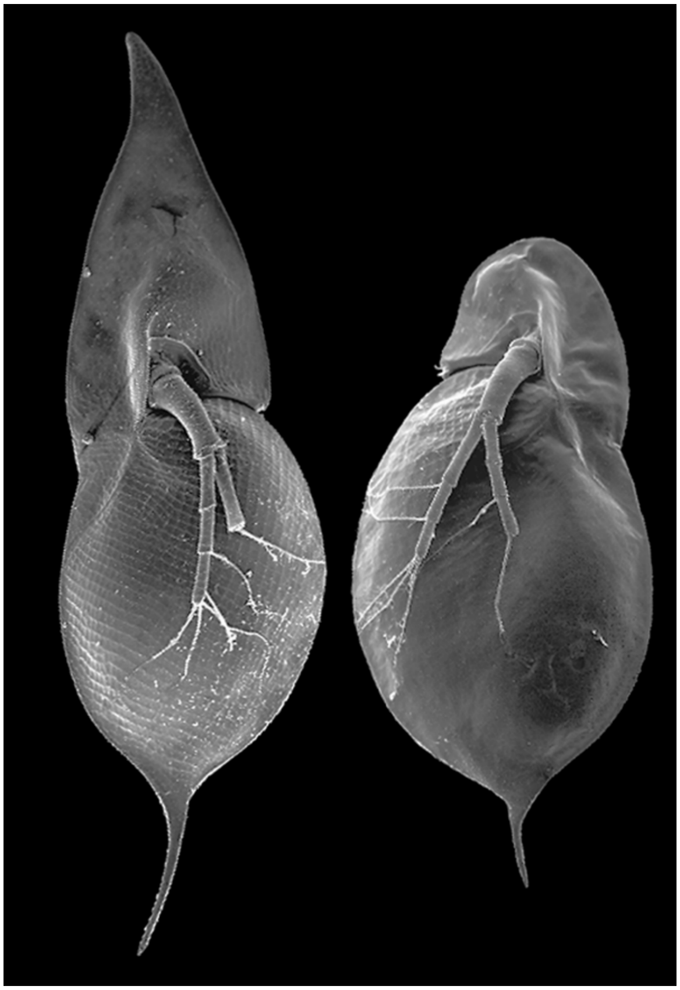

FIGURE 1 Scanning electron micrograph showing predator-induced (left) and typical (right) morphs of *Daphnia cucullata* of the same clone. *Note.* From "Transgenerational Induction of Defences in Animals and Plants," by A. A. Agrawal et al., 1999, *Nature*, 401, p. 61. Copyright 1999 by the Nature Publishing Group. Reprinted with permission.

ceived as an algorithm that learns how to survive and reproduce in a particular environment and stores that information in the genome. This accumulated information constitutes a strategy for survival and reproduction that is realized via ontogeny.

Realized ontogeny is not to be confused with the developmental strategy that gave rise to it. If we look at a chess player performing in a game, we see only what this player does under the specific circumstances of that game. It would take observations of many different games to infer the underlying strategy of the player if it exists. Similarly, one has to study the development of *Daphnia* under different circumstances to identify their developmental strategy. Although the variation in helmet development seems to be purely environmental, the underlying strategy is genetic. The genome specifies the ability to detect predators, the helmet developmental pathways that are contingent on predator detection, and the structure of the helmet that effectively limits predation.

THERE ARE DEVILS IN THE DETAILS: HOW IS A MOVE CHOSEN?

Biology is full of examples of divergent development of morphology and behavior. These examples raise challenging and subtle issues. In Pacific salmon, there are two distinct male phenotypes that differ in size and fighting ability (Gross, 1985). The larger male with superior fighting abilities is called *hooknose*; the smaller, weaker male is called *jack*. Jacks mature at age 1½, years and hooknoses mature 1 year later. Does a strategy underlie these differences? Biologists first thought that it is better to be big because this increases the ability to compete for females. Of course, they also had to explain why it would pay to be a jack. Females deposit their eggs in a nest at the spawning site. Males must quickly fertilize the eggs before others do. Quick access can be gained by two different moves: The first is to fight one's way to the nest; this is the move of the hooknose. The second is to hide behind a rock near the nest, wait until the female deposits her eggs, and then quickly dart out and fertilize some of them. Hiding is best done by a smaller fish, so this is the move of the jack.

Why would not all males be jacks or all hooknoses? If almost all males were hooknoses, the rare jack could easily fertilize eggs while the hooknoses were fighting. Conversely, if almost all males were jacks, they would run out of hiding places and the strong hooknose could easily keep the unhidden jacks away from the eggs. The success of a particular type is negatively dependent on its frequency. So, it is not astonishing that we observe the coexistence of two male phenotypes. But what causes a Pacific salmon male to become one type or the other? There are several qualitatively different ways in which type can be determined. First, there could be a genetic difference among the types that plays the role of the switch. Second, there could be a mechanism that flips a coin. Third, the male could use a cue that indicates which type would have more success given their current state.

The behavioral geneticist would emphasize that in the first case the phenotypic variation is completely explained by genetic variation, whereas phenotypic variation is completely explained by environmental variation in the other two cases (reality would be more complicated, of course). This standard analysis conceals the underlying similarity in strategy of all three cases. In all three cases, the hooknoses would have hooked jaws and canine-like teeth for fighting and a cartilage back shield for protection (these feature in jacks are less pronounced). Both hooknoses and jacks would possess most, if not all, of the genes for both types. The main difference would be only in the nature of the switch.

Biologists first thought that the switch was genetic, and breeding experiments seemed to support this view. Theoreticians emphasized both the genetic and coin flipping possibilities. However, further studies strengthened the case for a state-dependent switch (Gross, 1991). The facts are that if males have sufficient fat reserves (their state) at the age of 1½, they tend to become jacks. Otherwise they stay an additional year in the ocean to grow into hooknoses. The logic is that it is dangerous to stay in the ocean in the presence of predators, so one should leave for the spawning site as soon as possible. But it is also dangerous to lack the fat reserves needed to reach the spawning site. So one should not leave until one has accumulated enough reserves, and if this has not happened by age 1½, then one has to stay out in the ocean for an entire additional year. This affords it the opportunity to become much larger and paves the way for the specialized fighting adaptation of the hooknose.

Humans may also make moves based on their state. Sexual development does not occur until individuals begin to approach adult size. There are at least two possible strategic reasons for this. First, it is better to pay the cost of maintaining tissue, like enlarged breasts, only when this tissue is needed. Second, some aspects of the phenotype signal sexual maturity, and they would attract the attention of members of the opposite sex as well as same-sex competitors. This attention can be dangerous in some circumstances and is best avoided if one is not ready to compete for a mate.

SEXUAL DIFFERENTIATION

One of the most dramatic and widespread examples of developmental divergence is that of the sexes. The strategic aspects of this divergence have been recognized only in the past few decades. Because, in principle, females could reproduce without fertilization, it is not obvious why sexual reproduction has evolved. This issue has kept theoreticians busy for many years and is far beyond the scope of this article. But every approach to explain sexual reproduction uses the basic framework we outlined in this article—that is, to discover its strategic logic (see Ridley, 1995, for a very readable discussion of the issue). If we are willing to avoid this difficult issue by assuming sex exists, and it does, we can discuss some of the additional strategic aspects of sexual development. For simplicity we confine the discussion to placental mammals, including humans.

The major difference that biologically defines males and females is, of course, that between ovaries and testes. In placental mammals a fertilized egg stays with the female; this sets the stage for an important strategic vulnerability of the female in which she is obliged to develop elaborate mechanisms to care for the embryo, such as the uterus and mammary glands, whereas the male in most mammalian species provides little or no benefit to the offspring. Why should the male not develop a mammary gland to help the female raise their mutual offspring? We know that even politically correct males are incapable of offering this service. This is a bit surprising because they possess the genes for mammary glands, and they have nipples, so why not use them?

Before addressing this question, it is important to discuss the nature of the switch that sets off the different developmental pathways of males and females. Sex determination starts with the process of fertilization of a mammalian egg. We compare this process with a lottery containing many "tickets," namely, sperm that bear X or Y chromosomes. The mother draws one at random, the one that fertilizes her egg. Depending on the ticket, the developmental trajectory will go one way or the other, initiating a cascade of events that make the sexes increasingly different. Because the Y chromosome has very few genes, males and females are genetically almost identical. Sex differences must therefore lie in the different patterns of gene regulation. At an abstract level one could say that each sex is one move of a single underlying strategy encoded in the genome.

The conventional wisdom in biology is that sexual differentiation evolved to prevent males from providing milk to infants so they can instead engage in other activities, such as fighting. The latter activity is more important for males than for females in many mammals because of the sexual differences in reproductive potential.[1] But why has natural selection placed many of the different specializations into only two packages, male and female? By simply changing the gene regulation pattern evolution could have uncoupled uteruses, mammary glands, and other sex specific specializations. We are skeptical that the bimodality of sex is simply a consequence of developmental constraints. The fact that female hyenas have a penis-like structure through which they copulate and give birth, for example, casts doubt on the idea that developmental constraints cannot be overcome by selection. Earlier, we also described dramatic within-sex dimorphisms in fig wasps and ants.

We think a strategic approach might explain the widespread pattern of two sexes better than any attempt that relies solely on developmental constraints. One possible strategic approach emphasizes who is left holding the bag—in this case,

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[1] Male fitness is primarily constrained by access to mates: Unlike females, males with exclusive access to large numbers of mates could produce correspondingly large numbers of offspring. Therefore, it is more worthwhile for males to devote more effort than females to competing for mates.

the fertilized egg. The spatial association with the fertilized egg puts one sex at a strategic disadvantage by facilitating the desertion of the other sex (Bowles & Hammerstein, 2003; Maynard Smith, 1978). Therefore, the sex left holding the bag needs to have all the tools necessary to care for the egg. In nature this sex is more often the female but is sometimes the male (e.g., a number of fish species). The human case is more complicated because both sexes are spatially associated with the zygote, and there is no culture in which males refrain completely from investing in offspring. It is possible that a division of labor argument explains the maintenance of many sexual differences, such as the absence of functional mammary glands in males. It is known from economics that in cooperative enterprises, such as parenting, division of labor can dramatically increase productivity. One sex might specialize in care of young infants, whereas the other specializes in providing services that are incompatible with infant care.

LEARNING AS A STRATEGY

It is usually thought that learning is purely a function of the brain, but there are other physiological systems that are also highly specialized for learning. The vertebrate immune system is a prime example. It has to deal with a wide range of pathogens and with the fact that many of them can evolve rapidly. Natural selection could not evolve specific responses against all pathogens, especially those that evolve within the host organism. Instead it has learned powerful abstractions that apply to most pathogens, namely, that they contain proteins that differ from the host proteins. It has evolved specialized cellular systems that learn to identify pathogens by detecting their foreign proteins. Other systems then eliminate the detected pathogen.

We can draw several lessons from the immune system. First, there is environmental variation that natural selection cannot respond to because it occurs on too short a time scale (e.g., the rapid evolution of pathogens). Second, despite rapid variation at one level, there is tremendous stability at another level (e.g., all pathogens contain foreign proteins). Thus, natural selection can produce a learning mechanism that takes advantage of the stable, albeit abstract, aspects of the environment. The immune system is not a generalized learning system, however, because it cannot learn how to avoid predators or how to ride a bicycle. Rather, it is a mechanism specialized for learning about a specific abstract domain.

What the immune system demonstrates so nicely is that some strategies incorporate substantial learning, but the strategies themselves are fixed in the genome. The strategy, therefore, is a robust aspect of organismic design, whereas the use of the strategy results in flexible adaptive responses to highly variable environments. Learning can thus be seen as an extreme case of the simple developmental switches we discussed in the earlier examples.

Psychological learning mechanisms should reflect the principles we have deduced from the immune system. They should be scrutinized for features that reflect specialization to domains that are highly variable at one level but highly stable at a more abstract level (cf. Hagen, in press). Fear learning appears to correspond to these principles. It is specialized for domains that were dangerous to humans over evolutionary time, like venomous animals and heights, but not for novel dangers, like cars, guns, and electric outlets (Öhman & Mineka, 2001). Conditional learning is another example. At one level, the combinations of stimuli that co-occur are numerous and change relatively frequently compared with evolution. These combinations cannot all be learned by natural selection. At a higher level of abstraction, however, it is a stable property of the world that stimuli that have co-occurred repeatedly in the past are likely to co-occur in the future, at least within generations if not across them. If one of a pair of associated stimuli is highly relevant to fitness (e.g., food or a spider), it can pay fitness dividends to learn associations of that stimulus with other, arbitrary stimuli. This tactic can be learned by natural selection, and it has been: Conditional learning mechanisms are found in numerous species.

CULTURE AND THE RETURN OF LAMARCK

Learning is an adaptation to environmental variation that is too rapid for natural selection to respond. But some variation is slow enough that there is scope for adaptive intergenerational learning via nongenetic modes of transmission. A strategic view on development would predict the evolution of such Lamarckian mechanisms as a consequence of Darwinian natural selection operating on genes. So, in our view it would be a mistake to pit Darwinism against Lamarckianism, but it would also be a mistake to put them at the same level. Lamarck's theory of evolution by the inheritance of acquired traits is not an alternative to Darwin's theory of evolution by natural selection; instead, mechanisms with a Lamarckian flavor can evolve by natural selection.

Some species of water fleas nicely demonstrate the link between Darwin and Lamarck. Not only do these water fleas develop larger helmets in the presence of predators, as we already described, they also develop larger helmets even if they have not detected predators but their mothers have (Agrawal et al., 1999). This transgenerational induction of defenses makes strategic sense if the presence of predators varies on a time scale longer than an individual life span but short enough that natural selection favors a developmental switching mechanism.

Human culture is the most dramatic of all Lamarckian phenomena known to biology, and yet its principles have much in common with the development of helmets in water fleas. If the environment varied too rapidly, it would be pointless to listen to one's parents—as our generation has discovered—because their knowledge would be out of date. In contrast, if the environment did not vary at all, natural selection would simply equip everyone with the innate knowledge they need to survive and reproduce. The fact that humans have sophisticated adaptations for cultural transmission strongly suggests that significant environmental variability on the time scale of a relatively small number of generations played an important role in human evolution (Richerson, Boyd, & Bettinger, 2001).

There are also within-generation arguments for culture. If learning is very costly in time, effort, or risk, it may pay to imitate competitors instead of learning for oneself. But this cannot be a complete explanation for culture because those who imitate competitors are essentially parasites exploiting the efforts of others who paid the cost to acquire useful information. Due to this parasitism, the average fitness of a population with imitators will be no higher than a population with only individual learners (Rogers, 1988). Boyd and Richerson (1995) argued that the dramatic increase in the geographical range and population size of hominids, starting with the appearance of *Homo* about 2 million years ago and continuing to the present, means that the average fitness of the *Homo* population has increased. They believed this increase is due to culture. If so, then culture must be more than just imitation; culture must increase the average fitness of the population, and one way to do this is to improve individual learning itself. If instead of learning everything from scratch learners initially copy someone with expertise, they will under many circumstances reach a better solution more quickly or even a solution that would be impossible by individual learning. In this model, therefore, everyone is both a learner and an imitator. This can lead to the cumulative cultural evolution that characterizes humans. As much as the strategic approach to development can explain the evolution of the capacity for culture, once culture exists the cultural evolution of ideas can lead individuals and populations astray, for example, by sacrificing children to the gods. See Henrich and McElreath (2003) for a nice review of evolutionary approaches to cultural evolution.

CONCLUSION

Environments have many stable features but also exhibit important variation. The variation is often highly patterned, so that natural selection can evolve a developmental strategy to cope with it. This strategy—a list of moves that are conditional on fitness-relevant environmental circumstances—is ultimately coded in the genome. Within a species, the strategy is often broadly similar across individuals. In some cases, there are few, if any, important differences in genomes; thus, every individual possesses a nearly identical strategy. In other cases, a subpopulation will have a version of the genome that differs in certain aspects from other subpopulations.

To drive home our main point, we consider only an idealized species in which every individual has an identical genome and thus an identical strategy. Even in this case, individual phenotypes can exhibit significant adaptive diversity. Although the strategy is the same, each individual will make a different series of moves during development as he or she encounters different environmental circumstances at different times—a phenotype is a state of play. It is the robust genome-encoded strategy that enables adaptive phenotypic flexibility. Imagine a strategy with only 10 independent binary moves. This single strategy could potentially result in over 1,000 different phenotypes.

Sometimes a developmental move will result in differences in morphology that have little impact on behavior, but other times a move could result in changes to neuromorphology—the structure of the brain—that will have important behavioral consequences. Switches and knobs could alter morphological and psychological developmental trajectories throughout the life course. We agree with developmental psychologists that there will be multiple human developmental trajectories. We want to distance ourselves, however, from the idea, popular with some, that development is generally plastic. The term *plasticity* as used in everyday language evokes an almost infinite malleability with little underlying logic. This describes wax, not humans. Most modern neuroscientists and psychologists understand well that the brain cannot be shaped like wax and that important principles guide development (e.g., Baltes 1997). We believe that the term plasticity is ill chosen exactly for this reason. The evolutionary strategic view considers these developmental principles to be evolved strategies whose conditionalities enable the organism to develop adaptive, functional responses to highly variable environments. According to this view, flexibility does not reveal the absence of genetic influence but just the opposite. Wearing evolutionary biologist's glasses allows one to better see the evolved functionality of flexibility that is encoded in the genes.

Lifetime success in reproduction cannot be learned in the same way that success in chess can be learned. With chess, one knows whether one has won, lost, or drawn within a few hours (or perhaps days), and it is therefore possible to learn how to improve one's strategy in ontogenetic time by playing hundreds or thousand of matches. With lifetime reproduction, an individual has only one shot. Thus, it is not possible to improve one's performance in the reproduction game by individual learning. Natural selection, which experiments on an entire population for many hundreds and thousands of generations, can learn how to play this game very well indeed, and the strategy it has devised for us influences almost every aspect of our phenotype. Because cultural evolution, like natural selection, relies on transgenerational transmission of information, it can also learn how to play this game. Human reproduction depends on a complex and poorly understood combination of strategies learned by natural selection and cultural evolution. For a taste of some of the controversies about the application of the strategic view to social relationships, see Hammerstein (2003).

Although the strategy learned by natural selection is genetically encoded, we do not need to identify particular genes to study it. Instead, we usually examine the ontogenetic products of the genome, not the genome itself. The strategic logic of the heart and lung, as well as that of many of the examples we discussed here, can be perceived in their functional *design*—the physical structures of these organs—and the way in which these structures articulate with features of the environment (Williams, 1966). We advocate the view that the strategy is the appropriate unit of analysis for the study of human development, and the strategy will reflect the properties of the physical, social, and cultural environments in which humans evolved.

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