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### Author

Baum, WM

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## Chapter 24

# c0024 Behavior Analysis, Darwinian Evolutionary Processes, and the Diversity of Human Behavior

William M. Baum<sup>1,2</sup>

<sup>1</sup>University of New Hampshire, Durham, NH, United States; <sup>2</sup>University of California, Davis, CA, United States

p0015 The diversity of human behavior stems from three Darwinian evolutionary processes: genetic evolution, cultural evolution, and behavioral evolution. Genetic evolution by natural selection is the paradigmatic example of descent with modification or selection by consequences (Skinner, 1981). Cultural evolution accounts for the diversity of practices across groups and through time (Boyd and Richerson, 1985). Behavioral evolution, the third example of selection by consequences, also called “shaping” of behavior, occurs within the lifetime of an individual, and is a primary focus of behavior analysis.

p0020 The science of behavior, or behavior analysis, is properly part of evolutionary biology. It is intimately tied to evolutionary theory in two fundamental ways. First, evolution is the explanation of why behavior and behavioral processes exist at all. It is the only way to understand the peculiarities and constraints that characterize matters like classical and operant conditioning (Baum, 2013). Second, behavioral explanations follow the same mode of explanation as do evolutionary explanations. Skinner (1981) called it “selection by consequences.” It may also be called “historical explanation” (Baum and Heath, 1992).

p0025 Several writers have suggested that operant conditioning, or behavioral shaping, may be seen as parallel to natural selection. Donahoe (1999) suggests that even Thorndike may have recognized the resemblance between the law of effect and natural selection at the end of the 19th century. Skinner (1953, 1981) stated it overtly and made it the centerpiece to his view of behavior (Ringen, 1999). Gilbert (1970) drew out the parallel at length, and Staddon and Simmelhag (1971; Staddon, 1973) enlarged on it by distinguishing between “principles of variation”—ie, those

processes that give rise to behavioral variants—and “principles of selection”—those processes that cause selection among behavioral variants. More recently, Hull et al. (2001), used the term “interactor” to apply both to organisms in genetic evolution and to behavioral units in behavioral evolution, and again compared behavioral evolution to genetic evolution. The parallel is of more than casual interest; it represents a revolution in thought.

## POPULATION THINKING

The importance of selection and history has been underappreciated in the study of behavior within the traditions of psychology. One reason is that psychology, like other sciences, was influenced by philosophical views in which the world is thought to be composed of ideal types into which all particulars may be classified. In biology, typological thinking affected the concept of species. In psychology, typological thinking affected the concept of response, the unit of behavior. In biology, typological thinking eventually gave way to population thinking, which is the cornerstone of evolutionary theory and all selectionist theories. The difference between the two ways of thinking may be seen in their views on variation. In typological thinking, variation is “error” and dealt with as a nuisance to be eliminated by averaging. In population thinking, variation is central, and averaging is only an analytic convenience. As Ernst Mayr (1959) wrote, “For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real” (p. 2). Arguably, Skinner’s greatest contribution to the study of behavior was his

s0010

p0030

rejection of the typological view of behavioral units (responses). Mayr (1970) observed, “The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biology” (p. 5). The same may be said of the (ongoing) revolution in the study of behavior.

p0035 From an ontological point of view, a population is an individual—that is, an integral, functioning entity that can change and still retain its identity (Ghiselin, 1997). An individual is a whole with parts—as opposed to a class or category with criteria and instances. An individual changes when its parts change. The parts of a population are its members, and the population changes when its parts change. The population of mice in a particular meadow is an individual and is composed of the mice there. If the proportion of dark-colored mice increases relative to the proportion of light-colored mice, the population has changed or evolved, but it is still the population of mice in that meadow.

p0040 Population thinking means the appreciation of populations as units of evolutionary change. Evolutionary theory would be impossible without it. Darwin explained the origin of species by conceiving of species as comprised of populations that change across generations. The idea of change in the composition of a population allowed evolution to be explained as descent with modification, the result of variation with consequences for reproductive success.

p0045 The explanation of behavior as an outcome of selection by consequences similarly requires thinking about behavior as comprised of individuals with parts that may change (Baum, 2001, 2004, 2013; Glenn et al., 1992). Only if behavioral change is seen as change in the composition of a behavioral individual may it be explained as descent with modification. The behavioral analog to a population of organisms is an activity, because an activity is an individual with parts that may change when the parts change (Baum, 2002, 2004). A group’s pottery manufacturing is an activity with parts like obtaining clay, processing the clay, shaping the clay, decorating the pot, and firing. If, say, the decorations or type of clay changed, the activity of manufacturing pottery will have changed. My tennis playing is an activity with parts like buying equipment, serving, positioning, and returning the ball. My serving may change if I toss the ball in the air differently or swing my racquet differently, and if my serving changes, my tennis playing changes. Behavior analysts think of changes in activities as the result of contingencies between activity parts and phylogenetically important events, and the effect of contingencies is often labeled “selection by consequences” (Baum, 2012; Skinner, 1981).

p0050 Taking the unit of change as an individual—population or activity—allows one to think of evolutionary change as descent with modification. To have explanatory power,

however, descent with modification or selection by consequences requires identification of an evolutionary process. Plausibility requires construction of specific explanations, which require specific mechanisms (Hull, 1988).

## DARWINIAN EVOLUTIONARY PROCESS s0015

A Darwinian evolutionary process includes three basic elements: variation, recurrence, and selection. Each is necessary, and together they suffice to ensure evolutionary change (ie, descent with modification). p0055

## Variation s0020

Variation occurs within an individual thought of as a population or pool. A population of mice may be conceived of as a pool of genes, each mouse containing a set of genes, but because of recombination, a pool sufficiently fluid that the individual mice may often be ignored for purposes of explaining change within the population. Within the pool, different genes have different effects. Some influence coat color, some lung capacity, and others the structure of the brain. The key variation within any such pool is the variation among units that affect the same trait but produce different phenotypic effects—for example, that influence coat color but cause coat color to be dark or light. Evolutionary change depends on the existence of substitutable variants. In genetic evolution, such substitutable variants are referred to as alleles. They are substitutable in the sense that one allele may replace another, and they are mutually exclusive in the sense that such replacement is all or none. Evolutionary change consists of change in the relative frequencies of substitutable variants within the pool or population. p0060

The substitutable variants in behavior are the smaller parts of more extended activities, and the total activity over a span of time constitutes the pool. A group’s pottery making over the course of a decade may include a variety of styles of decoration, and as time goes by, one of those styles may replace the others, changing the group’s pottery making. My tennis serving over the course of a year may include variation in how high I toss the ball, and in time one toss height may prevail, changing both my serving and my tennis playing. p0065

## Functional Definition s0025

The units within the pool are defined, not by their structure, but by their function—that is, by their effects. In genetic evolution, the question arises as to how to break the genome into the constituent units that influence phenotype (Dawkins, 1989a). Although DNA has structure, one cannot tell which pieces should be called genes just by examining the structure. According to Dawkins (1989b), p0070

a gene must have three properties: fidelity (faithful copying), longevity (long enough lifetime to be copied), and fecundity (frequent copying). The units that possess these properties, however, may be small or large pieces of DNA, may be contiguous in a chromosome or not, may even be in different chromosomes, and may even be in different organisms [as in Dawkins's example of parasites' affecting phenotypic traits in hosts (Dawkins, 1989a,b)]. Whatever pieces of DNA act in concert to produce the phenotypic effect may be said to be faithfully copied, to endure well enough to be copied, and to be frequently copied to constitute the gene. The alleles compete because they differ in fidelity, longevity, or fecundity. A degree of copying fidelity may be assumed, because it is necessary for transmission. Differences in longevity and fecundity, however, result from differences in the alleles' phenotypic effects. A darker coat color may increase its possessor's likelihood of surviving long enough to reproduce.

p0075 Phenotypic effects, though often thought of as effects on morphology, are better seen as effects on the environment (Dawkins, 1989a). A darker coat color affects the ability of predators to detect a mouse against the ground. All phenotypic effects are environmental effects, because they facilitate exploitation of resources, survival, or reproduction. The point becomes clearer if we focus on genetic effects on behavior. Building a better nest alters the environment of the nestlings. Dawkins uses the example of the beaver's dam construction, which creates the beaver pond and reduces risk of predation, and has a host of other good effects on the beaver's environment. Human beings change their environment in myriad ways, creating shelters, places for plants to grow, instructional institutions, and so on. All may be seen as effects on the environment that function (usually) to enhance exploitation of resources, survival, and reproduction.

p0080 This focus on function, in the form of environmental effects, solves what would otherwise be an intractable problem: how to define genes. In a broader view of selection by consequences, it solves the problem of defining the substitutable variants within the pool of variants.

p0085 The same problem of defining units arises in cultural evolution and in the evolution of individual behavior, both of which constitute Darwinian evolutionary processes. As a focus on the structure of DNA offers little guidance about the definition of genes, so the structure of cultural practices and individual operant activities tells little about how they should be defined. Not that structure is totally irrelevant; in all three processes, structure constrains the definitions. DNA sequences specify the ordering of strings of amino acids, different configurations coding for different amino acids. Cultural practices and individual activities divide along what Skinner (1938) called "natural lines of fracture" (p. 33), constrained by anatomy and arrangements in the nervous system. As the codons of DNA represent "natural

lines of fracture" and specify minimal units that may be aggregated into genes, so fixed-action patterns and the structure of bones and muscles constrain what may be aggregated into the substitutable variants of culture and individual operant behavior (Skinner, 1969). The making of a pot comprises motions of the fingers and hands, but only those motions that the structure of the fingers and hands allows. The physical motions, however, are little help when it comes to defining the evolutionary unit. That will be the making of a certain kind of pot, and the substitutable variants will be the making of other kinds of pot, some of which may leak less, may be easier to handle, or may serve a social function by virtue of design. These variants compete within the culture pool, just as alleles compete within the gene pool.

All three units—genes, cultural practices, and individual operant activities—are defined in terms of environmental effects. All three are defined by what they accomplish in the world with which they make contact. Dawkins (1989a) made this clear about genes in his discussion of "extended phenotype." Guerin (1997) clarified the point for cultural practices when he argued that the functional unit of culture is "getting a job done." Every culture comprises "jobs" that must get done. At the most general level, the jobs might be reproduction, obtaining resources, protection from weather and enemies, and maintaining group cohesion. These general jobs subsume more specific jobs, such as child rearing, transport, and ownership. Whatever the level of generality that suits the analysis of culture, the substitutable variants will be different ways of getting the same job done. Different ways of raising children, of transporting oneself and goods, or of demonstrating group membership may compete with one another and may differ in their outcomes. Skinner (1938, 1953, 1957) explicitly defined operant "responses" (activities here) according to their environmental effects. One might say, following Guerin (1997), that a rat's lever pressing gets a job done. Although depression of a lever constitutes a discrete unit of behavior, more extended patterns produce more extended results. In the laboratory, several presses may be required for a bit of food, constituting a larger unit. In the everyday world, extended accomplishments always entail more specific accomplishments. Helping an unhappy customer entails listening to the complaint, making suggestions, talking to suppliers, and so on. Making a living might entail finding a job, going to work every day, specifying one's duties, and so on. Giving directions entails various utterances—statements about location, queries, and descriptions of action. Different ways of helping the customer, of making a living, or of giving directions constitute substitutable variants that may compete and may differ in their results. A customer may come away more satisfied, one may make a better living, and directions may be given more clearly.

### s0030 Pooling

p0095 All three processes, genetic, cultural, and behavioral evolution, require a pool of variation that includes substitutable variants. In general, the pool generates a frequency distribution—a profile of the frequencies of various types—that may change with time. For talking about evolutionary change, the important relative frequencies are those of the substitutable variants. Change results from competition. Fig. 24.1 illustrates the general idea. The top diagram represents a hypothetical pool, within which are substitutable variants A, B, C, and D, which occur at different frequencies. They could represent four different alleles for four different structures of an enzyme, or four different ways to catch termites (eg, with fingers, with a leaf, with a stick, or with a leaf stem). The relative frequencies are shown in the middle graph (open bars; the shaded bars will be discussed later). Allele (variant) B occurs at the highest frequency, then C, then D, and the least frequent is allele A. This pattern of relative frequencies may remain stable with time or may change, depending on selection.

p0100 Whereas the middle panel of Fig. 24.1 assumes discontinuous variation, the open bars in the bottom panel illustrate a hypothetical frequency distribution for variation fine enough to be considered continuous. It could represent variation in the genes affecting height or variation in squeezing clay that affects the thickness of the walls of pots. Although the variants cannot be grouped into discrete categories, they still exhibit a pattern of frequencies that may remain stable or change, depending on selection.

p0105 Fig. 24.1 illustrates the general idea of a pool characterized by a pattern of frequencies, which constitutes the essential element of variation in any Darwinian evolutionary process. Genetic evolution, cultural evolution, and behavioral evolution (shaping) all assume such a pattern of variation, although they differ in details, such as whether the units are localized or extended and whether variation is continuous or discontinuous. Genes are usually thought of as particular locations on chromosomes (ie, localized units) and alleles as differing in physical structure (ie, varying discontinuously), but when enough genes act in concert and vary, the substitutable variation becomes (approximately) continuous. Under some circumstances, such as parthenogenesis, the unit of variation may even be the entire genome (Dawkins, 1989a). Then the substitutable variation is certain to seem continuous. Although Dawkins (1989a,b) suggested a discrete unit of cultural variation analogous to the gene, the meme, nothing requires that the units of culture be localized or that variation in culture be discontinuous, any more than in genetic evolution. Boyd and Richerson (1985), for example, describe mathematical models of cultural evolution that assume variation to be

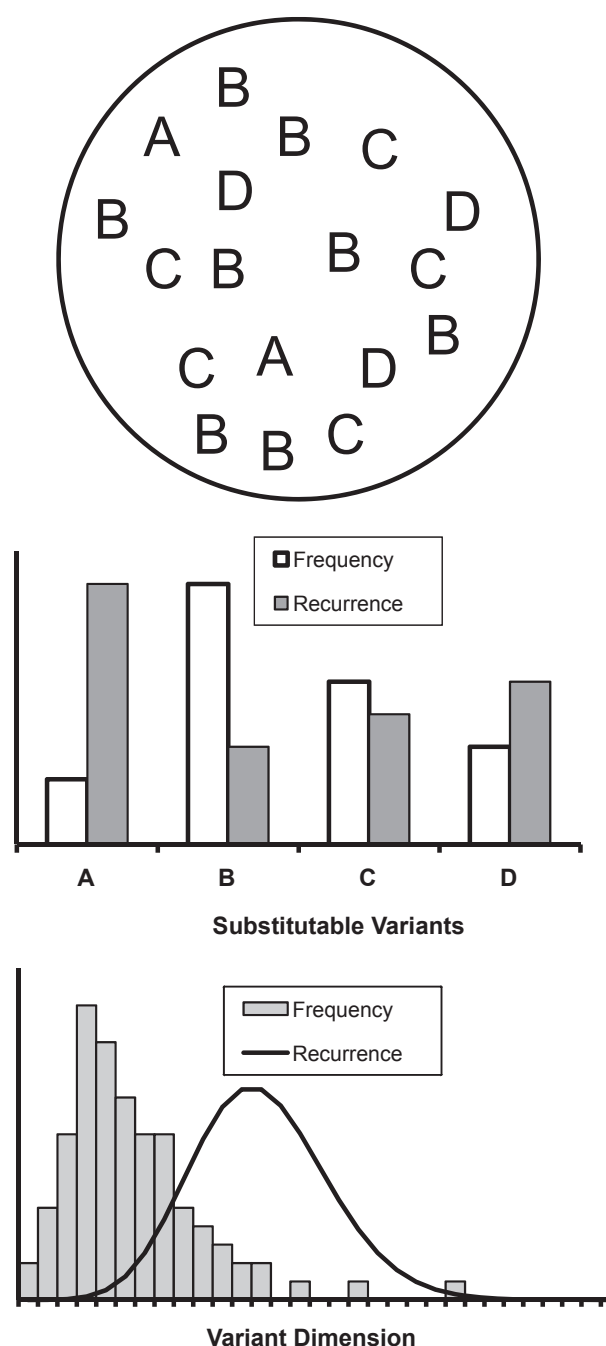


FIGURE 24.1 Population, frequency, and recurrence. Top: a population f0010 with four substitutable variants, A, B, C, and D. Middle: Frequencies and recurrences of the variants. Bottom: Frequency and recurrence with continuous variation.

continuous. In her classic book, *Patterns of Culture*, the anthropologist Ruth Benedict (1934) described the patterns of behavior in culture with the word “custom.” A custom or a practice cannot be localized to particular moments of time; it is an extended pattern of behavior that can only be observed over a substantial period.

p0110 With individual operant behavior, too, we are under no compulsion to assume discontinuous variation or localized units. That variation may be continuous is recognized in the study of response dimensions such as force, duration, and rate. The assumption that behavior must be defined in terms of momentary response units, however, has persisted for over 100 years. Nineteenth-century connectionism, in the forms of associationism and reflexology, promoted a view of behavior as composed of localized units such as ideas, sensations, and responses. That view was an accident of history, however, and may be overcome. [Baum and Rachlin \(1969\)](#), for example, suggested that behavior be divided into periods filled with various activities. Favorite responses of the laboratory, such as the lever press and the key peck, may be recast as activities, lever pressing and key pecking, which extend in time ([Baum, 1976](#)). [Rachlin \(1994\)](#) suggested that behavior generally be thought of as organized into patterns extended in time ([Baum, 1995a, 1997, 2002, 2004, 2013](#)). As with the customs of culture, an individual's daily behavior may be divided into activities like working, attending to family, and entertainment, none of which may be localized to moments in time.

p0115 Frequency distributions like those in [Fig. 24.1](#) presuppose that one may characterize the variation in a gene pool or behavior pool by taking a sort of snapshot of the frequencies at a moment in time. This might seem necessary for analytical purposes, because the frequencies may be changing. In practice, however, the snapshot is an abstraction, just as instantaneous velocity in physics is an abstraction, because any real sample is extended in time. In a gene pool, birth and death constantly alter the picture. For a behavioral pool, temporal extension is unavoidable. The customs of a culture or the habits of an individual cannot occur at a moment in time. The problem of taking a "snapshot" of frequencies is solved by choosing a time period long enough to provide an adequate sample but short enough that the pool may be thought of as unchanging for that duration. Depending on rate of change, one might gather data over a period of weeks, months, or years. As long as change in the pattern of frequencies during a period of sampling is negligible in comparison with change between samples, the course of change in the pool may be studied. That population thinking is central to genetic evolution has long been recognized. Population thinking, however, is equally central to understanding evolution of cultural behavior and individual operant behavior ([Glenn et al., 1992](#); [Hull et al., 2001](#)).

### s0035 *Cultural Practices and Individual Operant Behavior*

p0120 The line between cultural practices and operant behavior patterns may be fine. Indeed, [Skinner \(1981\)](#) argued that cultural patterns are operant patterns. Since cultural practices

presumably are maintained by their consequences, they might be considered operant patterns by definition. They may be distinguished, however, for the purpose of discussing cultural evolution by two characteristics. First, cultural practices are the possession of a group. To be called a cultural practice, a behavior pattern must occur in the members of a group—possibly a subgroup within a larger group, but definitely in more than one individual. Second, cultural practices are transmitted from member to member in the group. Unlike individual operant patterns, which one may say are transmitted to the same individual at different times, cultural practices are transmitted from one individual to another and may occur in different individuals at the same time.

### Recurrence

s0040

Recurrence means "occurring again" or "coming up again." p0125  
It is a general term for the tendency of a type of unit to reappear, with variation, time after time in the population—a more general term than "replication," "transmission," or "retention" ([Baum, 2001](#); [Campbell, 1965](#)).

### *The "Copying" Metaphor*

s0045

Genetic evolution is usually taken as the paradigmatic p0130  
example of a Darwinian evolutionary process. As a prototype, genetic evolution has both advantages and disadvantages. An advantage is that it has received enough attention to be both familiar and relatively well understood. A disadvantage is that, being comparatively well understood, some of its peculiarities are too easily mistaken for properties of evolutionary processes in general. This is particularly true of its mode of recurrence, which is often described with the metaphor of "copying."

Evolutionary recurrence need little resemble copying a p0135  
page in a photocopier. The word "replication" may be a synonym for copying, but may also be equated to reconstruction, which, for DNA, would be closer to the mark. We know about the uncoiling of the strands and the assembling of amino acids into replicate strands, with some recombination and occasional errors. In meiosis, the entire genome is replicated and divided into haploid components at once. The entire haploid genome is passed as a whole to the next generation. We need to ask, however, which properties of genetic transmission are essential for evolution. Darwin knew nothing of what we know about genetics today. Yet he was the author of the theory of evolution. His ignorance of genetics in no way prevented him from seeing the role of recurrence.

Darwin understood what was necessary: that the traits p0140  
of parents tend to recur in offspring. More generally, the traits of one generation are passed on to the next generation. Even the words "parent," "offspring," and "generation"

impede generalization. The essential part is recurrence through time. Traits tend to “breed true.” In the gene pool of a population of mice, the genes that make for a dark coat tend to recur through time, with the result that dark coats tend to recur (and possibly lower predation rate). In the beavers’ gene pool, the genes that make for dam constructing tend to recur, and if substitutable variants exist, each variant tends to recur, although selection may favor one variant over others. True, the recurrence of genes is the result of the details of reproduction, and those details are essential to understanding many aspects of genetic evolution. For a general definition of evolutionary process, however, what counts is the tendency of types in a population to recur in time.

p0145 Today we forgive Darwin for having believed in the inheritance of acquired characteristics, but writers about culture point out that such inheritance does occur in cultural evolution (eg, [Boyd and Richerson, 1985](#)). Again, however, the mechanism of recurrence is only important for understanding the details of cultural evolution. That it entails the inheritance of acquired characteristics helps us to understand the ways in which cultural evolution differs from genetic evolution. It is faster, for example, because transmission may occur between any individuals, not just parents and offspring, and may occur throughout the lifetime of an individual. It occurs as a result of imitation and instruction, although we might argue about exactly what those processes entail ([Baum, 2000, 2005](#)). The key, however, is that if a potter makes a certain kind of pot, his students will make the same kind of pot, and their students also, and so on. The practice recurs through time in the culture’s pool of practices.

p0150 Suppose, instead of genetic evolution, we took behavioral evolution (ie, shaping) as the paradigmatic example of an evolutionary process. We would see immediately that copying or replication is just one means of recurrence. A pigeon in an experiment pecks at a key time after time. A person goes to work day after day. Too little is known about the nervous system to say what the mechanism is by which behavior recurs in the same organism from time to time. Luckily, we may proceed with studying behavior without having any idea how recurrence is accomplished. The situation resembles that in biology prior to the synthesis of genetics with evolution in the early part of the 20th century.

## s0050 *Imperfect Recurrence*

p0155 Part of the reason for variation is that recurrence is often imperfect. [Hull \(1988\)](#) defines a replicator as “an entity that passes on its structure largely intact in successive replications” (p. 408). A paraphrase for the sake of generality might substitute “recurrences” for “replications.” Emphasis, however, should fall on the word “largely.”

Accidents happen. In genetic evolution, reconstruction of DNA sometimes goes awry. In cultural evolution, imitation and instruction may be inexact. In behavioral evolution, too, variation is intrinsic to recurrence, because context never exactly repeats, reconstruction even of a stereotyped activity like key pecking varies, and accidents happen. Recurrence need only have high fidelity; it need not be perfect. Indeed, one might argue that it must be imperfect, if the pool is to include sufficient variation to produce novelty. Without novel types, a pool’s response to selection must eventually cease.

## *Recurrence in Behavior*

s0055

In genetic and cultural evolution, the units (genes or practices) may outlive their possessors (their “vehicles” in [Dawkins’s \(1989b\)](#) parlance; their “interactors” in [Hull’s \(1988\)](#)). Individual operant behavior, in contrast, must die with its possessor—by definition, because if it lived on in others, it would be considered cultural. In no way, however, does this disqualify behavioral shaping as an evolutionary process. The key elements remain: a pool of variation, substitutable variants, and recurrence of variants through time. The frequency distributions in [Fig. 24.1](#) might describe genetic variation, cultural variation, or behavioral variation. Whether they remain stable or change with time depends on their relation to selection.

p0160

## *Selection*

s0060

The key to selection is differential recurrence. If substitutable variant A1 tends, on the average and over time, to recur more frequently than A2, the relative frequency of A1 increases at the expense of the relative frequency of A2. This happens if the size of the pool of variants is fixed or increases more slowly than the variants’ rate of recurrence. Usually one assumes the pool size to be fixed, because the size of a population of mice, for example, is limited by the environment’s carrying capacity—that is, the resources available to support the population. A behavioral pool, of cultural variants or individual behavioral variants, is fixed by limits on time, because only so much behavior can occur in a 24 h day. Consequently, when one substitutable variant increases in frequency, another must decrease. If one variant is more successful, it tends to replace the other.

p0165

One substitutable variant succeeds over another by virtue of superior environmental effects. For genetic evolution, this is where longevity and fecundity come in. Genes endure if their vehicles (interactors) endure, and recur if their vehicles (interactors) reproduce. The specific reasons for enhanced recurrence may be extremely varied—better defending or capturing of resources, better avoidance of predators, better defense against parasites, better mate selection, more mates, more offspring, better

p0170

care of offspring, and so on. All of these superior environmental effects ultimately increase the recurrence of the alleles that produce them and thus decrease the recurrence of the less successful alleles. For cultural and behavioral evolution, the same sorts of environmental effects act on the pool, but less directly and, therefore, with some slippage.

### s0065 *Selection in Culture*

p0175 The consequences of cultural practices that vary, making one variant more successful than another, may be thought of as reinforcers and punishers. Practices are maintained proximally by social reinforcement and punishment (Baum, 1995b, 2000, 2005; Skinner, 1981). “Our group shuns the eating of pork” is backed up with punishment (eg, disapproval, ostracism) for eating pork. “This mode of adornment is correct” is backed up with reinforcement (eg, status, mating opportunities) for adorning oneself so. Ultimately, the maintaining and differentiating social reinforcement and punishment are cashed out in terms of reproductive success of the vehicles (interactors) that carry the genes producing susceptibility to social consequences (“docility”; Simon, 1990). If group membership is beneficial to reproductive success, then group cohesion and cooperation are beneficial, and practices that make for group cohesion and cooperation are selected as a result of the members’ docility—their susceptibility to social consequences. Indeed, Boyd and Richerson (1992) demonstrated theoretically that social punishment allows selection of cooperation and just about any other behavior salutary to the group. [This summary omits other adaptations, such as sensory specializations and imitation (Baum, 2000, 2005).]

p0180 Dawkins (1989b) argued that the slippage between proximal social consequences and ultimate reproductive consequences allows cultural evolution to proceed independently of genetic evolution. The logic of genetic evolution goes against such a view (El Mouden et al., 2014). If some alleles make for more docility than others, the most successful alleles lie somewhere in the middle of the range of possible levels of docility, somewhere between none and “anything goes.” Too much docility means too little certainty of reproduction, because too much docility allows the spread and maintenance of customs that reduce reproduction. Thus, ultimately, alleles producing too much docility are selected against. (Boyd and Richerson (1985) make a similar point in their discussion of the tension between imitation and individual learning.)

p0185 One factor that curbs docility is primary reinforcement and punishment. As Dawkins (1989b, p. 57) suggests, consequences like “sweet taste in the mouth, orgasm, mild temperature, smiling child” or “various sorts of pain, nausea, empty stomach, screaming child” may have a genetic base because their presence generally affects the

likelihood of successful reproduction. Such stimuli constitute proximate tokens of ultimate reproductive success or failure, called elsewhere phylogenetically important events (PIE; Baum, 2005, 2012). If an interactor (vehicle) could be put together that would increase any behavior that produced the good environmental effects (circumstances that enhance reproductive success) and avoided the bad environmental effects (circumstances that depress reproductive success), such an interactor (vehicle) would prosper, and genes it carried would be more likely to recur in subsequent generations. As a result, genes that make for susceptibility to reinforcement by fitness-enhancing PIEs are selected. As a result, neither individual behavior nor cultural customs will stray too far from patterns that maintain the frequency of those PIEs. They will stray, however, for two reasons. First, the PIEs’ bearing on reproductive success is far from certain. Sweet taste is a reinforcer, and some consumption causes no problems, but overindulgence in sweets undermines health. Second, PIEs may conflict with one another. The same behavior that produces a smiling child may also produce an empty stomach. Which should win out may be far from clear; only the calculus of long-term reproduction can tell. When short-term and long-term consequences conflict this way, dysfunctional behavior may arise (Baum, 2016; Rachlin, 1995). Whether it persists or not depends on whether patterns that enhance fitness in the long run, such as eating fruits and vegetables, replace the dysfunctional ones, such as eating junk food (Baum, 2000, 2005, 2015; Rachlin, 1995). Although a person may die before dysfunctional behavior is replaced, correction in culture lies under no such limitation. It may take a few generations.

### *Primacy of Reproductive Success*

s0070

Maladaptive customs tend to drop out of the culture pool p0190 for two reasons: first, because failure to correct results in natural selection. Those who overindulge in sweets tend to become sick with diabetes and leave fewer offspring as a result (Diamond, 1992). Maladaptive customs decrease in frequency when their vehicles (interactors) leave fewer descendants to continue the customs. Groups that follow dangerous or abstinent practices, such as Quantrill’s Raiders or the Shakers, tend to disappear. Second, but probably more important, is that maladaptive customs contrast with their competitors (substitutable variants) in the calculus of reinforcement and punishment—ie, in the tokens of fitness. Prohibition in the United States was a response to the ruinous effects of overindulgence in alcohol; today educational campaigns encourage patterns of moderation or abstinence, based on better quality of life. When a maladaptive custom like smoking tobacco spreads through a culture because of short-term reinforcement, its long-term punishing effects eventually come into focus in

the form of social contingencies that punish it more immediately (or reinforce alternatives like nicotine patches more immediately).

p0195 The power of reinforcers and punishers as tokens of long-term reproductive success makes persistence of maladaptive customs unlikely. The genetic underpinnings of reinforcement and punishment argue against Dawkins's (1989a,b) conjecture that cultural evolution proceeds independently of genetic evolution. The genes that underlie learning and culture open the door, so to speak, to environmental influence, but they do not fling it wide.

p0200 Selection in all three processes—genetic, cultural, and behavioral evolution—may be traced back to reproductive success of genetic variants. In genetic evolution, the relation is direct; in cultural and behavioral evolution, the relation is less direct, but still present. When genes that make behavior sensitive to its consequences are selected, that must mean that the advantages of behavioral flexibility outweigh the costs it imposes in terms of energy and risk of error. If not, competitor genes that allow less flexibility would prevail. So, tokens of reproductive success (PIEs) attain the status of reinforcers, because variation in the environment rewards flexibility in the means to them. Signs of health, resources, and social relationships became powerful reinforcers, because the interactors (vehicles) for which they were reinforcers reproduced more often. A parallel argument applies to punishers, such as nausea, pain, snakes, and frowns. The same mechanisms of reinforcement and punishment that select among substitutable variants in behavioral evolution select also in cultural evolution. The differences are that cultural evolution entails transmission from individual to individual—imitation and instruction—and therefore depends heavily on social stimuli for provenance, and social reinforcement and punishment for selection.

p0205 In all three of the processes we are discussing, a question arises about the extent of the vehicles or interactors. Hull (1988) defines an interactor as “an entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication [ie, recurrence] to be differential” (p. 408; italics in the original; bracketed material added). But how large a unit can interact as a “cohesive whole”? Group selection has been treated with skepticism among evolutionary biologists, because it should normally be too weak to have much effect on gene frequencies. To work, it would require that gene flow into the group be negligible. That might be true of colonies of eusocial insects, for example (Seeley, 1989), but it would be unlikely for most groups, because of immigration of new members into the group. In cultural evolution, group cohesion is more likely, because imitation and instruction maintain a high degree of conformity within the group, even if new members join (Boyd and Richerson, 1992). In cultural group selection, groups with certain practices (eg, a

type of food cultivation or cooperation in obtaining resources) may out-compete other groups. The advantaged group may increase in frequency if it reproduces by fission and if competing groups tend to dissolve.

In evolution of individual operant behavior, where the distinction between replicators and interactors disappears, the analog to group selection is the temporally extended contingency. Extended contingencies are often discussed in terms of delays of reinforcement. The more temporally extended the behavioral pattern, the more delayed the consequences. Alternatively, one may consider delay to be incidental and the crucial aspect of extended patterns to be their cohesiveness. Extended behavioral patterns, such as eating a good diet, are notoriously difficult to maintain. Rachlin (1995) argues that good extended patterns (often called “self-control”) have a greater long-term payoff than short-term patterns (called “impulsiveness” or “defections” from the larger pattern). A defection from eating a good diet—eating an ice cream sundae—has an immediate payoff, but poorer consequences in the long run than eating a good diet (Baum, 2016). Selection on extended patterns is weak for the same reason that group selection on genes is weak. The boundaries of the group or of the extended pattern tend to be permeable—to immigration or to defection—the greater the permeability, the weaker is selection. This may be overcome in behavioral evolution by introducing relatively short-term contingencies that maintain the extended pattern intact (eg, reminders about one's diet).

### Why not Phenotypic Plasticity?

s0075

To explain the variation of culture or behavior from one environment to another, the alternative to selection is phenotypic plasticity. Cosmides and Tooby (1992) and Tooby and Cosmides (1992), for example, put forward the idea that the human brain contains a large number of “modules,” “algorithms,” or “mechanisms” that produce behavior depending on environmental conditions. They contend, “If human thought falls into recurrent patterns from place to place and from time to time, this is because it is the expression of, and anchored in, universal psychological mechanisms” (p. 216). They refer to such patterns as “evoked culture.” The conception has been compared to a jukebox containing recordings that can be played whenever called upon (Wilson, 1999). When food availability is highly variable, the “social contract algorithm” plays out food sharing; when food availability is stable, the jukebox plays keeping food within the family. Such explanations fail on two grounds. First, they are implausible. They exaggerate what is probably true, that genes constrain evolution of cultural practices and of individual behavior, to make a claim that would skip over the obvious effects of consequences on behavior. Instead of sensitivity to

feedback, they substitute input–output rules; given a certain environmental input, the mechanism produces a certain output. Such a view fails to explain an obvious fact: that culture evolves even if the environment remains constant. Second, alternative explanations are more plausible. If human behavior “falls into recurrent patterns,” that may be because of convergent cultural or behavioral evolution. Similar contingencies select similar behavior.

## s0080 Price’s Equation

p0220 **George Price** (1970, 1972) derived an equation, using straightforward algebra, that expresses precisely the meaning of natural selection. Imagine a population or group of  $N$  members at two time periods or “generations.” A trait or property of these members  $x$  varies among them. The trait could be the presence ( $x = 1$ ) or absence ( $x = 0$ ) of a particular allele ( $x = 0, 0.5$ , or  $1.0$  for diploidy), or a quantitative trait like body size or coloration. At Time 1, the mean of  $x$  across individuals is  $\bar{x}$ . Each individual  $i$  contributes  $w_i$  surviving offspring to the population at Time 2— $i$ ’s fitness or recurrence. Define a variable  $v_i$  that equals  $w_i/\bar{w}$ , the relative fitness of  $i$ . Each  $v_i$  is a weight; their sum equals  $N$  and their mean equals  $1.0$ . The mean of  $x$  at Time 2  $\bar{x}'$  equals:

$$\sum_i v_i x_i / N + \sum_i v_i \Delta x_i / N,$$

where  $\Delta x_i$  is the change in  $x_i$  for member  $i$  from Time 1 to Time 2 due to imperfect fidelity of recurrence. Using the definition of covariance  $\left(\sum_i v_i x_i / N - \bar{v}\bar{x}\right)$ , and taking the difference,  $\Delta \bar{x} = \bar{x}' - \bar{x}$  leads to the simplest form of the Price equation (see [Price \(1970\)](#) and [McElreath and Boyd \(2007, Chapter 6\)](#) for more detail):

$$\Delta \bar{x} = \text{cov}(v_i, x_i) + E_v(\Delta x_i). \quad (24.1)$$

p0225 [Eq. \(24.1\)](#) says that the mean change in  $x$  equals the dependence of relative fitness on  $x_i$  plus an expected value that gives the mean change in  $x$  apart from the covariance. The covariance represents selection; if relative fitness varies positively with  $x_i$ ,  $\Delta \bar{x}$  is positive, and the trait increases in the population. If the covariance is negative, the trait decreases, and if the covariance is zero, the trait remains stable. The second term on the right, which expresses the tendency of  $x$  to change as it recurs from Time 1 to Time 2 due to factors usually rare or negligible (eg, mutation or meiotic drive), may be considered close to zero for genetic evolution.

p0230 Put in more general terms, [Eq. \(24.1\)](#) says that if recurrence is differential with respect to various levels of a trait and fidelity of recurrence is high, then the trait recurs increasingly (positive covariance) or recurs decreasingly (negative covariance) in the population. Since the equation

is an identity, it describes rather than predicts, but it is a valuable analytical tool for thinking about selection—for example, group selection.

Suppose that the group under consideration is one group p0235 among many, because the population is structured into groups. Since [Eq. \(24.1\)](#) does not depend on the sort of individuals, [Eq. \(24.1\)](#) would also apply to selection among groups. For the sake of clarity, we index groups with the subscript  $g$  and apply [Eq. \(24.1\)](#) to get an expression defining  $\Delta \bar{x}_g$  the change in average fitness of the group. The equation says that if the covariance between levels of  $x_g$  and relative fitness  $v_g$  is positive, a group with a higher mean of  $x$  increases in  $x$  and grows in size relative to other groups. For example, if darker coloration is advantageous in avoiding predators, a group with darker coloration will grow and become darker.

In applying [Eq. \(24.1\)](#) to group selection, however, the p0240 second term on the right,  $E_v(\Delta x_g)$ , is no longer negligible, because the change in  $x_g$  apart from group selection includes changes in individual members due to selection at the level of individual members. Recognizing that  $x_g$  is a mean across members in the group that may change from Time 1 to Time 2, we treat  $\Delta x_g$  the same way we treated  $\Delta x$  and arrive at:

$$\Delta \bar{x} = \text{cov}(v_g, x_g) + E_g[\text{cov}(v_{ig}, x_{ig}) + E_v(\Delta x_{ig})], \quad (24.2)$$

where the subscript  $ig$  indicates member  $i$  in group  $g$  (see [Henrich \(2004\)](#) and [McElreath and Boyd \(2007, Chapter 6\)](#) for more detail).

The right-hand side of [Eq. \(24.2\)](#) has two components: p0245 one for selection between groups and one for selection between members within groups, the expected value term. For genetic evolution, we may ignore the expected value of  $\Delta x_{ig}$  in [Eq. \(24.2\)](#) as we did the expected value of  $\Delta x_i$  in [Eq. \(24.1\)](#), because the change would be due to rare or negligible factors such as meiotic drive and mutation. [Eq. \(24.2\)](#) then simplifies to the sum of a covariance for between-group selection and expected value of covariance for within-group selection.

An alternative form of the Price equation that uses the p0250 algebraic relation between covariance and the regression coefficient  $\beta$  may further clarify understanding of group selection (see [Henrich \(2004\)](#) and [McElreath and Boyd \(2007, Chapter 6\)](#) for more detail):

$$\Delta \bar{x} = \beta(v_g, x_g) \text{var}(x_g) + E[\beta(v_{ig}, x_{ig}) \text{var}(x_{ig})]. \quad (24.3)$$

[Eq. \(24.3\)](#) makes clear that the dependence ( $\beta$ ) between p0255  $v$  and  $x$  and the variance in  $x$  must both be greater than zero for selection to occur. Each term on the right implies a role for each of the three ingredients of evolution: variation ( $\text{var}(x)$ ), selection ( $\beta$ ), and recurrence ( $v$ ).

When applied to genetic evolution, [Eq. \(24.3\)](#) clarifies p0260 why genes for altruistic and cooperative behavior are unlikely to be selected by genetic evolution on its own. Some

traits may have both between-group and within-group components that act in concert—both have positive  $\beta$ —such as body size (helpful in intergroup combat) or tendency to stay close to the rest of the group (avoiding predators). Genes for altruism or cooperation, however, though helpful for the group, tend to reduce the fitness of individuals that behave so. Thus,  $\beta$  is positive for between-group selection, but negative for within-group selection. Since variance across groups  $var(x_g)$  in particular is lowered by migration between groups, the groups have to be practically completely isolated for group selection to overcome negative individual selection. Since negative  $\beta$  is likely to be high for any individual incurring an immediate cost for helping or cooperating with strangers, and within-group variance  $var(x_{ig})$  is unlikely to be zero, even a small amount of migration between groups will ensure that between-group selection is smaller than the within-group selection, making  $\Delta\bar{x}$  negative.

p0265 Eqs. (24.1)–(24.3) may be applied to cultural evolution, too, with suitable changes in definition. A cultural practice that might be considered all or none (eg, allowing marriage between first cousins or not, eating pork or not, and primogeniture or not) would take the place of an allele that is present or not. As with genetic evolution, however, quantitative variation in a practice (eg, a ritual performed daily or less often, for longer or shorter duration, with more or less of some ingredient, etc.) would do just as well for the variable  $x$ .

p0270 Recurrence of a practice from Time 1 and Time 2 goes, not just vertically as in genetic evolution, but obliquely and horizontally also (Boyd and Richerson, 1985; Richerson et al., 2016). Teachers, coaches, ministers, and peers both model practices and instruct practices that have proven successful in gaining the proximate tokens of ultimate fitness (reinforcers and avoidance of punishers). Particularly if these influential people are prestigious and display the trappings of success, this modeling and instructing spur the recurrence of the practice at Time 2, denoted, as before,  $w_i$ . As before, too,  $v_i$  is relative recurrence,  $w_i/\bar{w}$ , and if covariance between  $v_i$  and  $x_i$  is positive, the practice spreads. The second term on the right might be considered nonnegligible if one wished to incorporate errors on the part of recipients, but usually may be considered negligible because errors would likely be insignificant compared with selection (see El Mouden et al. (2014; supplemental Document S1) for a detailed derivation of Eq. (24.1) for culture and further discussion).

p0275 Eq. (24.1) would be about the spread of a practice through a cultural group. If we think of cultural groups as parts of a larger population, they may compete with one another for resources and members. Eqs. (24.2) and (24.3) will apply, with the same changes in meaning of the variables. Eq. (24.2) contains the same two components of intergroup selection and within-group selection (El

Mouden et al., 2014; Henrich, 2004). If a cultural practice benefits the group, and the more members practice it, or the more members' increased  $x_g$  increases the prevalence of  $x_g$  in the group ( $v_g$ ), the more positive is the first term in Eq. (24.2). Whether the covariance in the second term is positive or negative depends on whether it is beneficial or harmful to the individual who engages in the practice.

To understand how an altruistic or cooperative practice p0280 can spread in a population, Eq. (24.3) shows what happens if the within-group covariance for members is negative. As with genetic group selection, the variances  $var(x_g)$  and  $var(x_{ig})$  are crucial. In cultural group selection, biases in imitation and instruction (“transmission biases”) that promote conformity lower  $var(x_{ig})$  to near zero, even in the face of considerable immigration between groups. For example, if immigrants into a group tend to adopt the practice that is most frequent or above average in the group or tend to adopt the practice of prestigious or successful group members, their conformity will keep  $var(x_{ig})$  low (Henrich, 2004). Thus, the cost to the individual represented by the negative covariance of the second term may be offset by the positive covariance for the group, and altruistic and cooperative practices can spread in the population. The group in which members sacrifice for the group will gain more resources than other groups and will increase in numbers at the expense of other groups (Henrich, 2004).

Eq. (24.2) represents “multilevel” selection, but just at p0285 two levels—groups and individuals (McElreath and Boyd, 2007, Chapter 6). A practice may have many parts, and some of these parts may change without the practice taking on a new identity. For example, a manufacturing process or a ritual may drop or add elements; the American Pledge of Allegiance after many years changed to include the words “under God,” but it is still the Pledge of Allegiance, and process improvement constantly upgrades manufacture of automobiles, but the practice remains the manufacture of automobiles (Baum, 2002). When practices change in their parts, one might consider a third level of selection: within-practice selection. In Eq. (24.2),  $\Delta x_{ig}$  may be treated as change due to competition among alternative parts within the practice and expanded as before to result in a three-term Price equation (McElreath and Boyd, 2007, Chapter 6).

As far as I know, no one has applied Price's equation to p0290 behavioral evolution. The entities that may vary would no longer be individual organisms, because we are dealing with the behavior of a single organism. The varying entities are time samples within a larger time interval that constitutes the population—seconds within a minute, minutes within an hour, hours within a day, weeks within a year, and so on (Baum, 1973, 2012). The variable  $x_i$  that differs across time samples may be occurrence or not of an activity, if the time samples are short, or rate or time taken up

by the activity, if the time samples are longer, or any other quantitative aspect of an activity. The mechanism of recurrence is induction, which for operant activities is based on positive covariance with reinforcers and negative covariance with punishers (Baum, 2012). Eq. (24.1) applied to behavioral evolution means that if time samples (indexed by  $i$ ) including more of an activity in Time Interval 1 correspond to relatively more such time samples in Time Interval 2 (ie, positive covariance with  $v_i$  in Eq. (24.1)), then the activity ( $\bar{x}$ ) increases from Time Interval 1 (Population 1) to Time Interval 2 (Population 2)— $\Delta\bar{x}$  is positive. In a laboratory example, if a rat's rate of lever pressing is measured in 2 min intervals, the rate varies and may increase from 1 h to the next (Baum, 2012, Fig. 17). If a person's life changes by having children, spending more time with family daily in a period (population) of a month may vary positively with relative recurrence  $v_i$  in the next month, and the amount of time spent with family increases from month to month.

p0295 As with cultural group selection, Eqs. (24.2) and (24.3) apply to operant activities at a level or time scale of selection that may include selection at a lower level or shorter time scale. Cultural practices are, after all, operant activities. In an ontological perspective, operant activities and cultural practices are individuals with parts that work together to serve a function (Baum, 2002; Ghiselin, 1997). The analog to group selection is selection of whole activities extended in time, like playing tennis well or poorly and relating to one's spouse well or poorly. The analog of within-group selection is the selection of parts referred to earlier, because every activity is composed of parts that are themselves activities on a smaller time scale (Baum, 2002, 2012; Baum and Davison, 2004). Thus, the second term in Eq. (24.2) for behavioral evolution represents selection among parts of an activity. A tennis player's serve may improve when the ball is thrown up in a new way, and that variant may be selected. Active listening may improve one's relationship with one's spouse and be selected to replace a passive stance.

p0300 Eq. (24.3) for behavioral evolution illuminates problems in self-control, including altruism and cooperation. The conflict between impulsivity and self-control translates into a positive first term on the right (self-control) and a negative second term (impulsivity). Avoiding a bad habit or cultivating a good habit (eg, refusing a drink or a piece of cake or visiting the dentist) entails the cost of forgoing immediate enjoyment or of immediate discomfort, whereas the extended pattern ( $x_g$ ; sobriety, dieting, or good health) has positive  $\beta$ , but the positive  $\beta$  must suffice to offset the negative  $\beta$  of the second term (for  $x_{ig}$ ). This offsetting may occur if  $var(x_{ig})$  is reduced to zero by following a rule that enforces good behavior (refusal of the drink or cake; doing the right thing) on particular occasions. Seen this way, altruism and cooperation are

examples of good habits with immediate cost and long-term benefit (Baum, 2016; Rachlin, 1995, 2002).

Price's equation is incomplete or limited in two ways. p0305 First, it relies on linear regression (Price, 1970). The full-range relation between  $x_i$  and  $v_i$  may be nonlinear; often it will approach an asymptote, because a stable level of  $x$  in a population, due to dominance or frequency-dependent selection, will go along with reduced variance in  $v_i$ . When the population reaches equilibrium, the covariance between  $v_i$  and  $x_i$  disappears. Thus, Price's equation only has meaning when a population is in the process of evolving and we consider a limited range of  $x_i$  over which the relation between  $v_i$  and  $x_i$  is approximately linear. It doesn't apply to the whole process of change toward equilibrium. Second, by focusing on one particular allele, trait, or variable, the equation ignores the fate of other, competing variants. In all three evolutionary processes, if one variant increases, usually others must decrease. Competition implies a limit—carrying capacity for genetic evolution, fixed or slowly growing population for cultural evolution, and fixed time interval for behavioral evolution. A complete picture requires considering the fates of all the substitutable, competing, variants.

## EVOLUTIONARY EXPLANATIONS OF BEHAVIOR s0085

Mayr (1961) distinguished between proximate and ultimate crosref0485 explanations of behavior. Alcock (1993) incorporated the distinction into a textbook on animal behavior. According to Alcock, proximate explanations explain “how mechanisms *within* an animal operate, enabling the creature to behave in a certain way” (p. 2; emphasis in the original). Ultimate explanations explain how those mechanisms evolved as a result of selection. Proximate explanations refer to physiology and development. Ultimate explanations refer to history and reproductive success.

### Genetic Proximate and Ultimate Explanations s0090

Proximate explanations are about individual organisms, p0315 whereas ultimate explanations are about populations. The question, “Why do beavers build dams?” may be answered in two different ways. In one interpretation, the account would refer to stimuli from water and trees, the structure of the nervous system, hormones, and so on. It would explain how the cluster of genes that make for dam building express themselves in physiology and interact with the environment to ensure that Beaver X, alive today, builds a dam. That would be a proximate explanation. The ultimate explanation, in contrast, would make no reference to Beaver X, but would be about beavers as a species or about a population of beavers or about the gene pool of a

population of beavers, to which Beaver X or its genes might belong. It would refer to the adaptive consequences of building dams, variation within populations long ago, and increase in the frequency of alleles promoting dam building. It would explain how those alleles became common in the gene pool. Proximate explanations are silent about where the mechanisms for dam building came from. Ultimate explanations are silent about Beaver X, except to say that Beaver X builds a dam because it is the nature of beavers to build dams, and then to explain where that nature came from. So to speak, ultimate explanations are about the forest, whereas proximate explanations are about the trees.

p0320 Proximate explanations explain the behavior of individual organisms in terms of present mechanisms, whereas ultimate explanations explain patterns of frequency within a pool, such as those shown in Fig. 24.1, in terms of a process of differential success. Proximate explanations refer to causes in the present, whereas ultimate explanations rely on processes that may be called historical, because they extend in time (Baum and Heath, 1992). Evolutionary change results from continual operation of the process of selection over a period of time. That it takes time may be incidental, because it is a process of adjustment with a beginning in a disturbance (in the environment or in the population) and an end in a stabilized population. It is understood as a whole; at any point in-between, it is incomplete. Suppose the shaded bars in the middle panel of Fig. 24.1 represent the relative rates of success (recurrence) from one time period (eg, generation) to the next. Although variant A is lowest in frequency, it has the highest rate of recurrence. Given this pattern, we expect the frequency of variant A to increase, and the frequencies of B, C, and D to decrease. If relative recurrence is independent of frequency, the process will be incomplete until A dominates. (If relative recurrence is frequency dependent, a different equilibrium results, but that in no way affects this discussion.) Suppose the curve in the lower panel of Fig. 24.1 shows relative recurrence for the continuous case. The situation is essentially the same; we expect the frequency distribution to shift to the right. Eventually, we expect its maximum to coincide with the maximum of the curve; then the distribution stabilizes, and selection acts to keep it stable.

## s0095 Cultural Proximate and Ultimate Explanations

p0325 Since every evolutionary process includes the distinction between the mechanism that produces the advantageous behavior and the history of advantage for that behavior, cultural evolution and behavioral evolution also admit of the distinction between proximate and ultimate explanations (Alessi, 1992). In cultural evolution, the mechanism by which a custom is transmitted explains why it persists

(ie, why it recurs), whereas the prevalence of the custom ultimately lies in a history of competition and selection. As with the question, “Why do beavers build dams?” the question, “Why does this tribe adorn themselves with tattoos?” may be interpreted and answered in two different ways. In the proximate interpretation, the question might be reworded as, “Why do the members of the Hell’s Angels motorcycle club wear the club’s tattoos?” Alternatively, “Why does Tom, who belongs to Hell’s Angels, wear the tattoos?” Three or more mechanisms of transmission might be involved. Tom might imitate other members of the tribe. Other members might instruct Tom: “If you want to be accepted, you should get the tattoos.” Once Tom began getting tattoos, reinforcement from tribe members might lead to getting more tattoos. In the ultimate interpretation, the question might be reworded as, “How did it come about that the Hell’s Angels wear those tattoos?” The answer would refer to the history of selection in the culture pool. Tattooing may have competed with other forms of adornment, such as wearing black jackets, wearing hair in a ponytail, or speaking in a certain dialect. One or two members may have gotten tattoos. Other members who saw them frequently may have imitated them as a result. Boyd and Richerson (1985) call this *frequency-dependent bias*. The first members with tattoos may have been imitated by the other members or may have been able to instruct the other members because they held high status in the club. Boyd and Richerson (1985) call this tendency to imitate success *indirect bias*. Tattooing may have worked better to identify members because other groups might wear black jackets or ponytails and because dialects vary from region to region; tattoos are permanent and unambiguous. Boyd and Richerson (1985) would call reinforcement of a custom by such an environmental effect *direct bias*. Any combination of indirect bias, frequency-dependent bias, and direct bias would result in an increase in the frequency of wearing tattoos among the tribe, until the wearing of tattoos became virtually universal.

## Nesting of Evolutionary Processes

s0100

Genetic evolution may be thought of as an overlay on p0330 cultural evolution. Ultimate and proximate genetic explanations may be constructed for the question, “Why do the Hell’s Angels wear tattoos?” They would be analogous to the explanations of dam building in beavers. The proximate rewording of the question would be, “Why did Tom get himself tattooed?” As with Beaver X, the explanation refers to stimuli (eg, from the behavior of other members), reinforcers (eg, from the other members), development (eg, early exposure to Hell’s Angels), and physiology (eg, brain mechanisms)—all of which might be traced to gene expression. The genetic ultimate explanation rewords the question as, “How is the wearing of tattoos beneficial to the

members of the tribe?" The answer might be that it constitutes symbolic marking of the group, distinguishing it and promoting cohesion within it, which in turn promotes group selection for various forms of cooperation, which enhance the success of the group and thus boost the members' reproductive success. It would include also the advantages to alleles that make for frequency-dependent bias, indirect bias, and direct bias in competition with alleles that do not (Boyd and Richerson, 1985; Richerson and Boyd, 2000). Other stories might be told, but they would all end with the same reference to reproductive success, because in a genetic ultimate explanation genes must be selected. The biasing effects of genes ensure that any custom that decreases reproductive success, even if common for a time, is likely to disappear eventually.

## s0105 The General Evolutionary Process

p0335 Fig. 24.2A diagrams an evolutionary process in general terms and shows the different focuses of proximate and ultimate explanations. Each of the variables,  $V$ ,  $F$ ,  $E$ , or  $R$ , may be thought of either as a pool of variants, as a frequency distribution across variants, or as a frequency of a particular variant relative to all others. In the parlance of cybernetics, they are operands and transforms, whereas the rectangles represent processes (transformations) that produce transforms from operands (Ashby, 1956). A pool of variants (process) results in  $V$ , a distribution of substitutable variants or relative frequency of a particular variant relative to all its competitors. A process of expression transforms  $V$  into  $F$ , a distribution of interactors (or vehicles) or frequency of one type of interactor relative to all others. The expression process receives input from the environment, omitted from Fig. 24.2 in the interest of simplicity. The input is represented by levels of variable  $N$  ( $N_1$ – $N_6$ ) in Fig. 24.3, which illustrates the various transformations in Fig. 24.2A. The top line of Fig. 24.3 shows  $V_i$  composed of three variants, A, B, and C, having equal frequencies. The different levels of the environmental variable  $N$  affect the outcomes in  $F_i$ ; so that B coupled with  $N_2$  goes to  $\alpha$ , the same outcome as A coupled with  $N_1$ , whereas B coupled with  $N_3$  goes to  $\beta$ , and C transforms to  $\beta$ ,  $\gamma$ , or  $\delta$ , depending on  $N$ . In this illustration, the variation in  $N$  results in a distribution  $F_i$  that has more variety than  $V_i$ .

p0340 A set of external standards or contingencies, which might be characterized as a set of if-then rules, transforms  $F$  into  $E$ , a distribution of external effects. These are shown in Fig. 24.3 as levels of  $W$ ,  $X$ ,  $Y$ , and  $Z$ , just to emphasize that they are transforms of the elements of  $F_i$ :  $W$  goes with  $\alpha$ ,  $X$  with  $\beta$ ,  $Y$  with  $\gamma$ , and  $Z$  with  $\delta$ . They may be thought of as levels of success—eg, reinforcer rates or numbers of matings.  $E$  feeds back to a recurrence process, which results in  $R_i$ , a distribution of recurrence rates or a relative recurrence rate. Following the example in Fig. 24.3, if the elements of

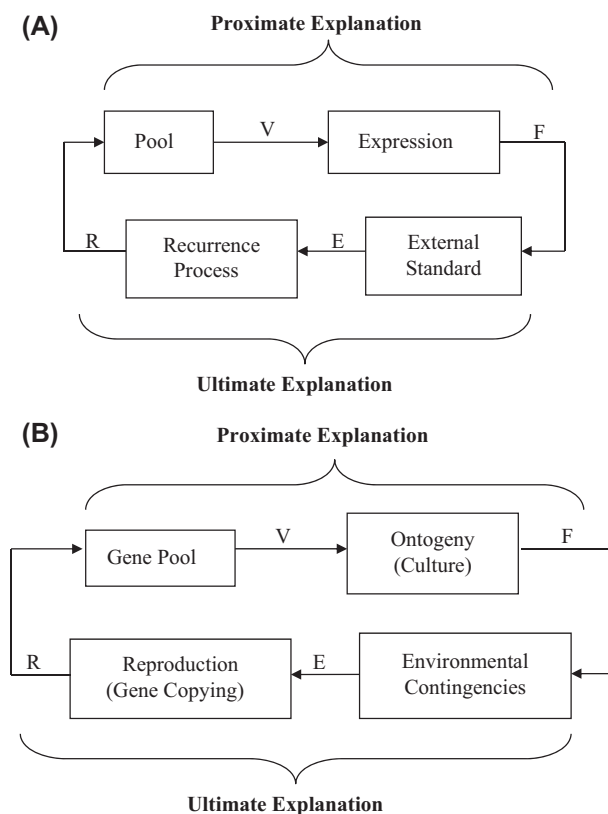
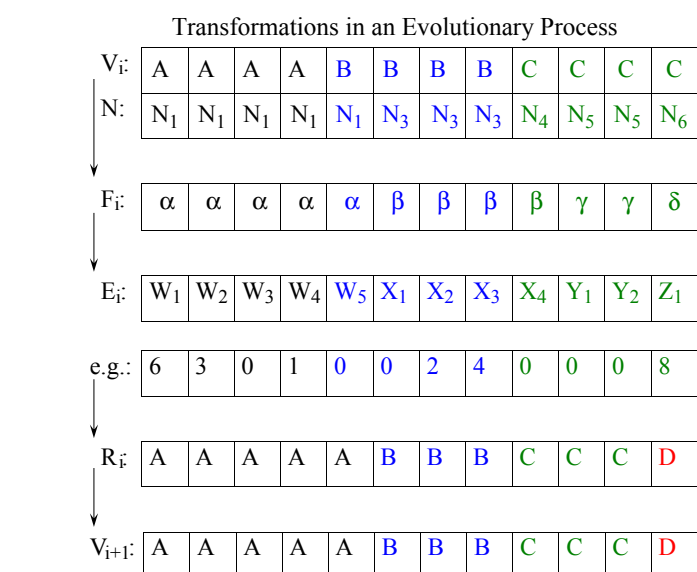


FIGURE 24.2 (A) The general evolutionary process as a flow chart. A f0015 distribution of substitutable variants,  $V$ , is transformed by expression into a distribution of interactors,  $F$ , which an external standard transforms into a distribution of effects,  $E$ , which recurrence transforms into a distribution of recurrences,  $R$ , which enters or replaces the pool to produce a new transform  $V$ . (B) The general evolutionary process chart applied to genetic evolution. A distribution of alleles ( $V$ ) is transformed by ontogeny (eg, culture) into a distribution of phenotypes ( $F$ ), which environmental contingencies transform into a distribution of environmental effects ( $E$ ), which gene copying transforms into a distribution of recurrences ( $R$ ), which updates the gene pool and produces a new distribution of alleles.

$E$  associated with A ( $W_1$ – $W_4$ ) have a collective weight of 10 ( $6 + 3 + 1$ ), those associated with B have a collective weight of 6, and those associated with C have a collective weight of 8 (entirely due to the fortunate occurrence of  $N_6$ , which resulted in transform  $\delta$  in  $F_i$ ), then the frequencies in  $R_i$  reflect these collective success rates. The appearance of variant D, however, has nothing to do with these success rates, but rather represents some kind of accident: a mutation, copying error, or external force.  $R_i$  closes the loop by entering the pooling process to result in the new distribution of variants  $V_{i+1}$ .

If this system is disturbed by a change in the pool (eg, p0345 mutation or immigration) or in the external standards (eg, a change in climate), resulting in disequilibrium like that depicted in Fig. 24.1, it will tend to move back toward equilibrium, because iterations of the feedback loop cause



**FIGURE 24.3** Illustration of the transformations of Fig. 24.2. In generation  $i$ , distribution  $V$  contains three substitutable variants, A, B, and C, with equal frequencies. The input  $N$  has six levels,  $N_1$ – $N_6$ , which enter the transformation to  $F$ , a distribution of interactors that contains four different interactors,  $\alpha$ ,  $\beta$ ,  $\gamma$ , and  $\delta$ , in unequal frequencies. This is transformed to a distribution of effects, labeled  $W$ ,  $X$ ,  $Y$ , and  $Z$  to correspond with  $\alpha$ ,  $\beta$ ,  $\gamma$ , and  $\delta$ . In the example, the effects for A,  $W_1$ – $W_4$ , sum to 10, the effects for B,  $W_5$ – $X_3$ , sum to 6, and the effects for C,  $X_4$ – $Z_1$ , sum to 8. These sums determine the frequencies in the distribution of recurrences  $R$ . A new variant (accident), D, also arises in  $R$ . In this example, the recurrence distribution for generation  $i$  becomes the distribution of substitutable variants for generation  $i + 1$ .

the composition of the pool to change until it comes into accord with the external standards—ie, to an optimal fit.

Fig. 24.2A also illuminates the roles of proximate and ultimate explanations (braces). The links from the pool to the external standards—ie, from  $V$  to  $F$ —constitute the focus of proximate explanations. They pose the question, “By what mechanisms does a distribution of variants result in a distribution of interactors?” The links from the external standards to the pool constitute the focus of ultimate explanations. They pose the question, “How does the distribution of external effects change the composition of the pool?” That is a question about selection. The diagram omits any explicit indication of the iterative nature of evolutionary change; that must be taken for granted. The reason that both proximate and ultimate explanations are necessary for a full understanding is that the two explanations address different parts of a whole process—mechanical connection and feedback, immediate causation, and history.

## s0110 Genetic Evolutionary Process

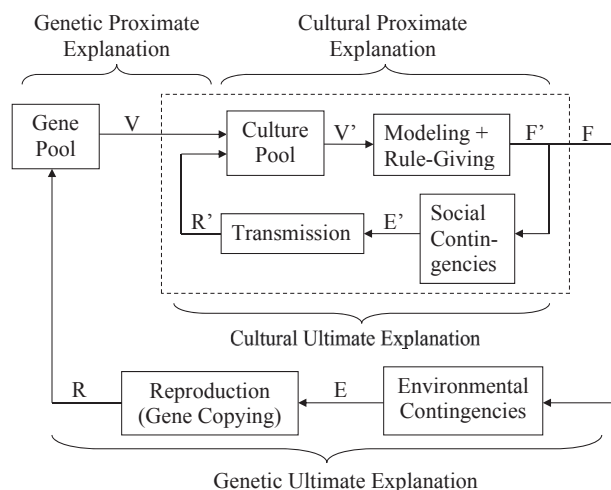
Fig. 24.2B shows the general diagram applied to genetic evolution. The gene pool offers a distribution ( $V$ ) of

genotypes. Ontogeny or development transforms  $V$  into a distribution ( $F$ ) of phenotypes. Environmental contingencies specify a distribution ( $E$ ) of environmental effects, such as rates of obtaining resources, of predation, or of mating. Reproduction, which may be thought of as gene copying, depends on  $E$ . Sometimes it is thought of as simple transmission of genes from parents to offspring, but it may also be complex, because it may be the locus of other forms of selection besides natural selection—eg, sexual selection. Its outcome  $R$ , the distribution of copying rates (fitnesses), in turn changes or maintains the composition of the gene pool. Proximate explanations focus on processes of ontogeny and development. Ultimate explanations focus on the feedback, the way the environmental contingencies and reproduction achieve selection among genotypes.

As an example, we may apply Fig. 24.2B to the evolution of culture—that is, the transition from a noncultural species to a cultural species as a result of genetic evolution (as opposed to cultural evolution, our second process). Ontogeny converted the distribution of genotypes  $V$  into a distribution of phenotypes ( $F$ ) that varied in ability and propensity for culture—that is, in the mechanisms that cause a group of people to have a culture (group-level behavior transmitted from member to member). Elsewhere I have argued that three mechanisms would suffice: sensory specializations, imitation, and social reinforcers (Baum, 2000, 2005). Whether or not these are the answer, they suggest the sort of mechanisms that would constitute a proximate explanation for the development of culture in children and newcomers to a group. The distribution  $F$  might be called “variations on culture.” A highly variable environment made culture beneficial to the hominids that possessed even its rudiments (Boyd and Richerson, 1985; Richerson and Boyd, 2000). It would, for example, solve many problems related to the obtaining of resources and mates. Those variants favored in the distribution of environmental effects ( $E$ ) would be more represented in distribution  $R$ , with the result that the genes underlying the mechanisms for culture would increase in the gene pool. That feedback would be the ultimate explanation for the existence of culture.

## Nesting Cultural Evolution Within Genetic Evolution

Fig. 24.4 diagrams the relationship between genetic evolution and cultural evolution and the different focuses of their proximate and ultimate explanations. It shows two feedback loops: an outer loop symbolizing genetic evolution and an inner loop (enclosed in the box) symbolizing cultural evolution (cf. Burgos, 1997). The inner loop takes the place of ontogeny in Fig. 24.2B or expression in Fig. 24.2A. The culture pool may be thought of as all the



**FIGURE 24.4** The cultural evolutionary process as an example of the general process (Fig. 24.2A) and as nested within the genetic evolutionary process. The rectangle of broken lines demarcates the cultural process. A distribution of all cultural variants (practices) available  $V'$  is transformed into a distribution of actually occurring variants  $F'$  by induction (eg, modeling) and rule-giving (“instruction”). The distribution  $F'$  comes into contact with social contingencies, which transform it into a distribution of social effects (reinforcement and punishment),  $E'$ . The distribution of effects is transformed by transmission into a distribution of recurrences of the practices  $R'$ . The distribution of genetic variants that interact with culture  $V$  enters the culture pool as input, thus affecting  $V'$ . The distribution of actually occurring practices  $F'$  corresponds also to the distribution  $F$  that is the operand for environmental contingencies that form the context for the cultural process. The braces indicate the focuses of the different proximate and ultimate explanations.

customs present in the group—the potential variants, resulting in a distribution  $V'$ . One might be tempted to think of  $V'$  as a distribution of memes. Our ignorance of the workings of the brain suggests that temptation is best resisted (Baum, 2000; Simon and Baum, 2011). The mechanism of expression, labeled “Modeling + Rule-Giving,” embodies the vagaries of the social environment that transform  $V'$  into a distribution  $F'$  of actual cultural variants (customs). Models and rules are stimuli that may induce imitation and rule-following, behavior that may be reinforced or punished by group members (Baum, 2000). Alternatively, one might think of the culture pool as directly producing  $F'$ . (As before,  $F'$  could also represent the relative frequency of a particular custom.) The structure of the social environment, particularly social contingencies, results in a distribution  $E'$  of social consequences. For example, food sharing might result in approval, whereas food hoarding might result in disapproval or aggression. From  $E'$ , transmission results in a distribution  $R'$  of recurrences that feeds back to change or maintain the composition of the culture pool. The means of transmission are imitation and instruction (Baum, 2000, 2005). They constitute the locus where Boyd and Richerson’s (1985) indirect and frequency-dependent biases operate.

Fig. 24.4 depicts the way in which cultural evolution and genetic evolution may interact. The distribution  $F'$  interacts as  $F$  in the external loop (genetic evolution) with environmental contingencies to produce distribution  $E$ —that is, cultural practices may affect genetic evolution (Boyd and Richerson, 1985). If, for example, group members who shared food were more likely to marry, then any genes that promoted tendency to share food would be selected.

The braces in Fig. 24.4 indicate the different focuses of proximate and ultimate explanations in genetic and cultural evolution. Genetic proximate explanation focuses on the mechanisms by which genetic variants (distribution  $V$ ; shown as input to the cultural pooling process) affect cultural evolution. Cultural proximate explanation focuses on the mechanisms (possibly in the nervous system, but specifically related to behavior in groups) by which cultural variants (distribution  $F'$ ) are expressed. Modeling and exhortation, for example, might induce food sharing. Cultural ultimate explanation focuses on the iterative feedback from social consequences that shapes the culture pool over time. Once induced, for example, food sharing might be reinforced by approval, status, or reciprocation. Genetic ultimate explanation focuses on the feedback from environmental consequences of culture on the composition of the gene pool. It represents the feedback of culture on genes that prompts Boyd and Richerson (1985) to speak of “gene-culture co-evolution.” Failure to keep these four different types of explanation distinct is likely to result in confusion. For example, development (genetic proximate explanation) might account for the presence of imitation and instruction, which underlie cultural ultimate explanation of cultural change over time. Cosmides and Tooby’s (1992) idea that cultural variation can be explained by genetic expression probably arises from confusing these two types of explanation.

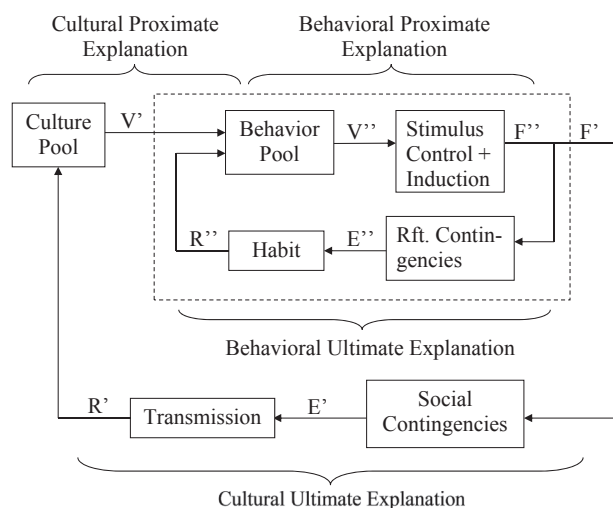
## Proximate and Ultimate Operant Explanations

In behavioral evolution (ie, shaping), the distinction between proximate and ultimate explanations is the distinction between physiological mechanism and history of reinforcement. Advantageous behavior is defined by reinforcement and punishment. Explaining the occurrence of advantageous behavior may refer to events in the nervous system or to the history of advantage. As with the other two evolutionary processes, a question like, “Why does Liz brush her teeth before she goes to bed?” has two interpretations. The proximate interpretation focuses on the mechanism: “On any particular night, what causes Liz’s tooth brushing?” The proximate explanation would focus on stimuli that regularly precede going to bed and tooth brushing and events in the nervous system that result from

these stimuli and cause tooth brushing at that time. The ultimate interpretation focuses on a history of selection: “How did it come about that Liz brushes her teeth before bed?” or “What advantage has Liz derived for brushing her teeth?” The ultimate explanation focuses on the differential consequences of tooth brushing in Liz’s life that selected tooth brushing at bedtime over other behavior that might have occurred at bedtime. It would refer to bedtimes in Liz’s childhood, her father’s exhortations, reprimands, and approval, and the later incorporation of tooth brushing into the pattern of behavior surrounding bedtime combined with events at the dentist’s office. Different stories might be told, but they would all refer to the advantages of tooth brushing over time.

### s0125 Nesting of Behavioral Evolution Within Cultural Evolution

p0385 Fig. 24.5 parallels Fig. 24.4, depicting the relationship between behavioral evolution and cultural evolution. The inner loop, behavioral evolution, contains the same elements as in Fig. 24.2A. It stands in the place of



f0030 **FIGURE 24.5** The operant (behavioral) evolutionary process as an example of the general process (Fig. 24.2A) and as nested within the cultural evolutionary process. The rectangle of broken lines demarcates the operant process. A distribution of all behavioral variants available  $V''$  is transformed into a distribution of actually occurring variants  $F''$  by stimulus control and induction (eg, by releasers). The distribution  $F''$  comes into contact with reinforcement contingencies, which transform it into a distribution of effects (reinforcement and punishment),  $E''$ . The distribution of effects is transformed by habit (ie, physiological mechanisms) into a distribution of recurrences of the behavioral variants  $R''$ . The distribution of cultural variants that interact with individual behavior  $V'$  enters the behavior pool as input, thus affecting  $V''$ . The distribution of actually occurring behavior  $F''$  corresponds also to the distribution  $F'$  that is the operand for social contingencies that form the context for the individual process. The braces indicate the focuses of the different proximate and ultimate explanations.

“Modeling + Rule-Giving” in Fig. 24.4 or “Expression” in Fig. 24.2A. The behavior pool consists of all the individual’s potential behavior—species-specific behavior plus all the behavior ever expressed in this individual. It results in a distribution  $V''$  of behavioral variants. The culture pool adds to the individual’s behavior pool via the distribution  $V'$ . The mechanisms of stimulus control, including induction, transform  $V''$  into a distribution (or relative frequency)  $F''$  of presently occurring behavior. Those mechanisms correspond to what Staddon and Simmelhag (1971) called “principles of variation.” The structure of the environment, in the form of contingencies of reinforcement and punishment (or reinforcement and punishment feedback functions; Baum, 1973, 1989, 2012), converts  $F''$  into a distribution  $E''$  of environmental effects, or consequences. These reinforcers and punishers constitute the relatively immediate tokens of ultimate reproductive success discussed earlier. Distributed differentially over behavioral variants, they result via mechanisms in the body, particularly in the nervous system, labeled “habit” in Fig. 24.5, in a distribution  $R''$  of (relative) recurrences, which in turn changes or maintains the composition of the behavior pool. The behavioral proximate explanation focuses on the stimuli and physiological mechanisms that cause the behavior on particular occasions. The behavioral ultimate explanation refers to the selective effect that the token consequences have on the mechanism and behavior over time. A proximate explanation of sharing meat with other group members would point to the occasion of returning to one’s village with a captured animal. The ultimate explanation would point to the history of exhortation in favor of sharing, social reinforcement for sharing, and punishment of hoarding. The effect of differential consequences on individuals’ behavior provides the means for the cultural effects that Boyd and Richerson (1985) call guided variation and direct bias. Guided variation names the contribution of individual innovation to the culture pool. For example, the individual who makes a better arrowhead may catch more food personally, but the method also may be incorporated into the culture pool by imitation and instruction. As we have already seen, direct bias is the effect of the token consequences on transmission of practices. The method of making the better arrowhead personally benefits anyone who uses it. The effect of behavioral evolution on cultural evolution is symbolized by the output of distribution  $F''$  as  $F'$  to cultural contingencies, which in turn produce  $E'$ , the distribution of social consequences.

Taken together, Figs. 24.4 and 24.5 suggest two levels p0390 of nesting. Evolution of individual operant behavior is nested within cultural evolution, which is nested within genetic evolution. To understand human behavior, one needs to attend to all three levels and to all the various proximate and ultimate explanations they imply.

p0395 In a noncultural species, the behavioral inner loop is directly nested within the genetic outer loop (cf. [Burgos, 1997](#)). In that situation, gene expression affects the mechanism that causes the behavior and is sensitive to feedback from the token consequences. As in cultural evolution, the token consequences affect gene copying, which feeds back on the composition of the gene pool, favoring alleles that promote the mechanism that allows behavioral evolution in the first place. If we ask why a laboratory rat presses a lever in an operant chamber, the answer might begin with an explanation of why the rat is so constructed that a contingency between presses and food pellets affects its behavior—ie, the advantages of learning by reinforcement ([Baum, 2005](#); [Donahoe, 1999](#); [Zeiler, 1999](#)).

### s0130 **An Example: Self-Control**

p0400 Behavior analysts have progressed on the problem of understanding self-control. Initially, it was analyzed as a conflict between deferred and immediate consequences ([Ainslie, 1974](#)). Self-control consists of choosing behavior that pays off in the long run over impulsiveness, which is behavior that pays off in the short run. For an alcoholic, acceptance of a drink is immediately reinforced, whereas abstinence, though it has a greater reward, is reinforced only at a great delay. The question remains, however, as to how the deferred consequences ever overcome the influence of the relatively immediate ones. How does self-control ever predominate? [Rachlin and Green \(1972\)](#) suggested one possibility: commitment. If one acts at an early time to prevent choosing impulsiveness (eg, having part of one's salary deposited directly to a savings account before one can spend it), then self-control becomes more likely when the choice arises. Most situations calling for self-control, however, offer no opportunity for commitment, because occasions for impulsiveness are frequent and unpredictable. Some alcoholics take drugs that produce noxious effects when alcohol is in the bloodstream, and some dieters have their jaws wired shut, but most people rely on other means.

p0405 [Rachlin \(1995\)](#) argued that self-control might be better understood if it were seen as a pattern of choices extended over time. Occasional impulsiveness ("defection" from the overall pattern) might occur without necessarily disrupting the extended pattern of "doing the right thing." The temporally extended pattern we call eating a healthy diet constitutes self-control even if it is peppered with minor defections like having an ice cream cone. The extended pattern, [Rachlin](#) argued, has a higher value—ie, produces greater reinforcement—than any defection. Those greater and temporally extended consequences explain the persistence of the pattern.

p0410 [Rachlin's \(1995\)](#) account stops, however, at an awkward place. Although it helps to frame the initial

question, it leaves the question unanswered: how does the pattern of self-control ever emerge and persist in the face of frequent opportunities for gaining immediate reinforcement for impulsiveness? In comparison with the contingencies favoring impulsiveness—powerful because of the relative immediacy of the reinforcement—the contingencies favoring self-control are weak and vulnerable because of their temporal extendedness, as in our comparison to group selection. How could the weak selection ever prevail?

That question raises at least two others: (1) why would p0415 an individual care about eating a healthy diet in the first place?; and (2) why would such a concern spread and persist among many members of a society? On the surface, the answers might seem obvious: quality of life and longevity. Quality of life, however, is a social construct, requiring explanation itself, and death cannot punish nor can longevity reinforce any subsequent operant behavior. Instead, the two questions may be interpreted as being about cultural and genetic evolution: (1) why do other members of a group promote and enforce eating a healthy diet?; and (2) how are genes selected that support acquisition and maintenance of behavior like eating a healthy diet? The answer to the first question requires identifying self-interest on the part of one member in other members' health. Such is near at hand, because practices concerning medicine and public health in advanced societies today are costly for the entire group (taxpayers, at least). The contingencies involved may be compared to those involved in so-called "altruism." We sacrifice to benefit others if greater benefit accrues to us eventually. The sacrificial behavior is dangerous, however, because of the possibility of cheating—ie, someone's reaping benefits without paying the cost. When most members contribute to the cost of maintaining health in all, poor health is analogous to cheating. Customs promoting and enforcing health-enhancing behavior are selected in such a social setting (see "social contingencies" in [Figs. 24.4 and 24.5](#)). The whole extended pattern of healthy eating is selected, in analogy to group selection, as in [Eq. \(24.2\)](#).

A possible way that genes might be selected that sup- p0420 port eating a healthy diet would be in response to variability in foods available from one environment to another. The advantages to imitation and easy instruction discussed earlier would apply to dietary habits. If you are an immigrant or child newly arrived in a group, the diet eaten by those around you is more likely to promote health than one you choose for yourself. Genes favoring imitation and easy instruction would be selected.

These suggested explanations are incomplete and may p0425 be incorrect, but they illustrate the sort of ultimate operant, cultural, and genetic explanations that an understanding of self-control requires. Many of the ideas are open to empirical study. They point to directions in research on behavior within an evolutionary framework.

## s0135 CONCLUSION

p0430 Viewed from a sufficiently general perspective, such as diagrammed in Fig. 24.2A, genetic, cultural, and behavioral evolution all may be seen as examples of the same sort of evolutionary process. Since all three allow the distinction between immediate causation of behavior and the historical origin of the causes, all three allow both proximate and ultimate explanations. Indeed, full understanding requires both proximate and ultimate explanations. The nesting of the three processes in the way suggested in Figs. 24.4 and 24.5 means that the study of culture needs not only to take account of cultural evolution, but to be aware of the constraints imposed by genetic evolution and the contributions of operant behavior and its evolution to cultural evolution. Similarly, the study of human behavior needs to take account of the constraints imposed by both cultural evolution and genetic evolution. A complete explanation of a behavioral pattern needs to go beyond the processes that govern individual behavior. It needs to specify the provenance of behavior in cultural customs and in genetic effects on development and to explain the origins of effective stimuli and consequences in cultural and genetic evolution.

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**Non-Print Items****Abstract**

The resemblance among behavioral evolution, cultural evolution, and genetic evolution emerges in the light of a general concept of evolutionary process. Every evolutionary process consists of three elements: variation, recurrence, and selection. Evolutionarily significant variation occurs among substitutable variants within a pool. Differences in environmental effects among variants produce differences in recurrence, and those differences feed back to affect the composition of the pool of variants. The three evolutionary processes may be nested: cultural evolution within genetic evolution, and behavioral evolution within cultural evolution. A complete understanding of human behavior requires proximate and ultimate explanations in all three processes.

**Keywords:**

Behavioral evolution; Cultural evolution; Evolution; General evolutionary process; Nested processes; Operant behavior; Proximate explanation; Substitutable variant; Ultimate explanation.