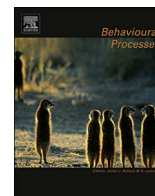




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# The non-Darwinian evolution of behaviors and behaviors<sup>☆</sup>

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## ABSTRACT

Many readers of this journal have been schooled in both Darwinian evolution and Skinnerian psychology, which have in common the vision of powerful control of their subjects by their sequela. Individuals of species that generate more successful offspring come to dominate their habitat; responses of those individuals that generate more reinforcers come to dominate the repertoire of the individual in that context. This is unarguable. What is questionable is how large a role these forces of selection play in the larger landscape of existing organisms and the repertoires of their individuals. Here it is argued that non-Darwinian and non-Skinnerian selection play much larger roles in both than the reader may appreciate. The argument is based on the history of, and recent advances in, microbiology. Lessons from that history re-illuminate the three putative domains of selection by consequences: The evolution of species, response repertoires, and cultures. It is argued that before, beneath, and after the cosmically brief but crucial epoch of Darwinian evolution that shaped creatures such as ourselves, non-Darwinian forces pervade all three domains.

## 1. Introduction

Most articles in this special issue will focus on the relevance of Darwinian evolution to our understanding of behavior. In all, it will be a foregone conclusion that learning, and the rich repertoire of behaviors and environmental sensitivities displayed by animals, are products of evolution.<sup>1</sup> This paper will address the sufficiency of Darwinian selection and the *Modern Synthesis* as models of how to think about, discuss, and model behavior and its evolution. Most<sup>2</sup> evolution is permeated by non-Darwinian<sup>3</sup> processes (Gontier, 2015), and some experts have argued that “random drift constrained by purifying [selection] in all likelihood contributes (much) more to genome evolution than Darwinian selection” (Koonin, 2009 p. 474). This paper reviews how that is so, and proposes that non-Darwinian mechanisms may provide more apt models for some behavioral processes, such as the competition and selection among responses of individual organisms, among the organisms themselves, and among their cultures. This exposition borrows heavily from the history of evolutionary thinking and the confounding role in it of the evolution of microbes—*prokaryotes* and *archaea*—found in the excellent *The New Foundations of Evolution; On the Tree of Life*, by Jan Sapp (2009). All unattributed page references are to quotations or

information derived from this book.

## 2. Essentialist pre-Darwinian thinking: form or function, essential or adapted?

Essentialist thinking, the Platonic notion that all the mundane forms are but low-pixel renditions of essential pure ideals, has tough going in modern hard-nosed empirical sciences such as behavior analysis. Yet it was a crucial early recognition of biologists that any hope of tracing evolutionary paths had to distinguish essential features from adapted, or adventitious, ones. In order to trace lines of descent, knowing which features are homologous—the wing of a bat and the foreleg of a dog—and which are analogous—the wing of a bat and the wing of a bird—is a prime requisite. The homologs share evolutionary origins, the analogs converge under evolutionary pressures. Whether to base taxonomies on similarity or on presumed evolutionary continuity was hotly debated through the 19th and most of the 20th centuries. As Lamarck (1809) argued, gradations in relatedness of essential features were “only perceptible in the main groups of the general series, and not in the species or even the genera” (p. 11). Individual species are too subject to convergent evolution and adaptations to unique

<sup>☆</sup> Note: This paper benefited greatly from the editorial process. One very negative reviewer helped me to clarify my thinking and writing; one positive reviewer gave me confidence that was worth trying to do. John Staddon showed me where my arguments were inconsistent, vague, or incomplete. Billy Baum helped me to put it all together, playing both editor and helpful keen-eyed reviewer. Blame none of them for what you read; and as you read, try to map that process of reading onto some of the schema in this paper, viz. transfer vs. selection.

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<sup>1</sup> For a thoughtful and enlightening review of selection in evolution, immunology, and behavior, see Hull et al. (2001).

<sup>2</sup> “Most”, in terms of numbers of replicating and evolving organisms, including prokaryotes.

<sup>3</sup> The name is ironic, as Darwin allowed inheritance of acquired characteristics and saltation, “non-Darwinian” modes; in contrast, Wallace rejected any role for Lamarckian processes in evolution. Yet the eponym has stuck.

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environments; a general sense of essential<sup>4</sup> features could only arise from study of families and orders. Fifty years later Darwin concurred: “It even may be given as a general rule that the less any part of the organism is concerned with special habits, the more important it becomes for classification” (p. 32).

Whereas the Linnaean taxonomy of visible organisms was well advanced by the 19th century (see Fig. 1), that of microbes was not. Taxonomies are important, because to argue for continuous evolution of species with modification through generations, one must have a reliable taxonomy of species, groups, and families. But this was not available for microbes. The problem was both ontological and epistemological: The first due to the nature of their evolution, and the second to the difficulties of studying them. Bacteria “live in such a complex, co-dependent way in the environment that the great majority could not be cultured in isolation from one another and characterized” (xiii). After a half-dozen proposed taxonomic schemes (one of which is shown in the central branch of Fig. 1), one well-received solution was a multi-dimensional similarity taxonomy called *Bergey’s Manual*, a long-lived, commonsensical, pragmatic, and authoritative handbook of microbes. But it was ad hoc. How, for instance, should one weight all the features that characterized a particular bacterium? The default of equal weighting was a weighting. With the advent of DNA sequencing it might be hoped that a genetically-based taxonomy might resolve the scores of taxonomies that had gone before with an evolutionarily-based one. But this was not to be the case, for reasons that are central to this paper.

### 2.1. Creatures void of form

The section title is from Sapp, with an obvious Progenitor. Microbes—Protista, protozoa, or any of a number of names for this newly recognized kingdom—were often simply called germs. It was unclear whether they were plants or animals, and in the last quarter of the 19th century much that was known about them came from the harm that they could do to humans and their kine—dysentery, anthrax, gonorrhoea, typhoid and so on (see Table 4.1 in Sapp for a depressing roster of discoveries). They were also known for some of the good things in life—the yeasts that give us bread, beer and wine, and for the liberation of nutrients from once living things through the processes of decomposition. Just as the Diagnostic and Statistical Manual of Mental Disorders (DSM) drives the categorization of human behavior in terms of what is broken and how to fix it, much of the study and classification of microbes depended on what good or harm they could do to us, what malign niche they inhabited; but as is the case for the DSM, this is not a good basis for scientific taxonomies. Whereas germs may be classified by such beneficent or maleficent properties, unlike macroscopic plants and animals they could not be classified by their form because they were pleomorphic. Bacteria showed diversity in only size and a few basic forms: spherical, rod, or spiral. These were of only limited help in taxonomies—whereas fine filters could separate bacteria, for example, some “filterable bacteria” were so small that they could pass through all filters. These came to be called *viruses*. Further clarification awaited electron microscopy.

### 2.2. Mineral, vegetable, or animal?

Although there was always some question as to whether viruses were living (prions, despite being replicating proteins, are judged not alive), there was never much question about the life of the other microbes. But were they little vegetables (now *protista*) or little animals

<sup>4</sup> Although some contemporary scholars took this in the Platonic sense of Natural Kinds, Lamarck, Darwin, and the present discussion takes its meaning as having the features which will support consistent tracing of evolutionary lineages—that have, if you will, substantial evolutionary momentum.

(*protozoa*)? To a certain extent that depended on whether you were a botanist or zoologist (Scamardella, 1999). Outsiders such as Copeland made a good attempt<sup>5</sup> at systematization (p. 74), but there was always an arbitrary character to such systems. Perhaps the solution would be delivered by the *modern synthesis* of Mendelian genetics with zoology, ecology, taxonomy, botany and paleontology.

### 3. The reality of species

The modern synthesis viewed selection as acting on variants within populations: Evolution was the change in the genetic constitution of those populations. The modern synthesis disallowed inheritance of acquired characteristics, and disallowed saltations—discontinuous jumps in complexity and genetic diversity.<sup>6</sup> Alas, bacteria acquired characteristics, as well as inheriting them, and passed both on. Microbes were not included in the new synthesis (p. 78). They were of too protean a nature,<sup>7</sup> and put a fine point on the question of whether species are real—natural groups. For Darwin and Lamarck (and see fn 4), species were not real—not immutable things with sharp boundaries. But “the reality of species was a cornerstone of the new systematics” (p. 80) deriving from the new synthesis. Dobzhansky referred to species as natural units, defined by the line at which two potentially interbreeding groups become separated into populations that are incapable of interbreeding; Mayr adopted this definition (adding the factor of geographical separation along with Dobzhansky’s mutual infertility) which he called “the biological species concept” (p. 81).

This concept could not be applied to asexual organisms, as bacteria were seen to be. The concept also ran into problems with plant hybridization, which was a significant mechanism of evolution in numerous groups of plants. As late as 1962 two experts wrote “the abiding intellectual scandal of bacteriology has been the absence of a clear concept of a bacterium” (p. 94; Selective replacement of two words will make that sentiment seem close to home to behavior analysts (Marr, 2009); as different substitutions would to cognitive psychologists, or to psychiatrists, or to .... We are not alone). It is perhaps more surprising that there is little agreement on how to define eukaryotic species: “there are multiple, inconsistent ways to divide biodiversity into species on the basis of multiple, conflicting species concepts [more than twenty extant schemes], without any obvious way of resolving the conflict. No single species concept seems adequate” (Richards, 2010).

Down below, the plot thickened when it was shown that viruses could transfer genes between bacteria; that some bacteria could incorporate the genes of dead bacteria that they consumed; that some “sex” (*conjugation*) occurs in *E. coli*; and that *Paramecium* could form cytoplasmic connections and exchange genes. There were exciting developments in the last half of the 20th century, such as the acceptance of the distinction between prokaryotes (bacteria and blue-green algae that lacked a nuclear membrane, and are one thousandth the size and

<sup>5</sup> His “successful and now rather widely followed” (Whittaker, 1969, 153) four-kingdom system was profoundly pragmatic: “The limits assigned to a particular group, one which is named, assigned to a definite taxonomic category, and defined by description, are always artificial, arbitrary, decided by convenience. Convenience at this point means something subordinate to the over-riding convenience, or necessity of recognizing groups which are natural. [1] A conservative element of convenience is familiarity: the taxonomist is loath to propose abandonment of a familiar arrangement unless he can propose [a better] one... [2] phyla and classes should not be too numerous; families and genera should not be too extensive. A third element of convenience lies in feasibility of definition by description; ... often attained by making limits coincide with “missing links,” that is, with breaches of knowledge. The formulation of a system of classification, then, involves a double set of hypotheses: hypotheses as to the ancestry, origin, and evolution of groups, and hypotheses as to what boundaries will be found expedient” (Copeland, 1938, 383–384). Copeland had excellent taste in how to balance these desiderata, to find the expedient.

<sup>6</sup> On both counts, different than Darwin’s theory, which allowed both “sports” and inheritance of acquired characteristics. “Non-Darwinian” here refers to “non-neo-Darwinian,” “non-Modern Synthesis” which disallow both.

<sup>7</sup> As one reviewer put it, “a horse of an indistinct color”.

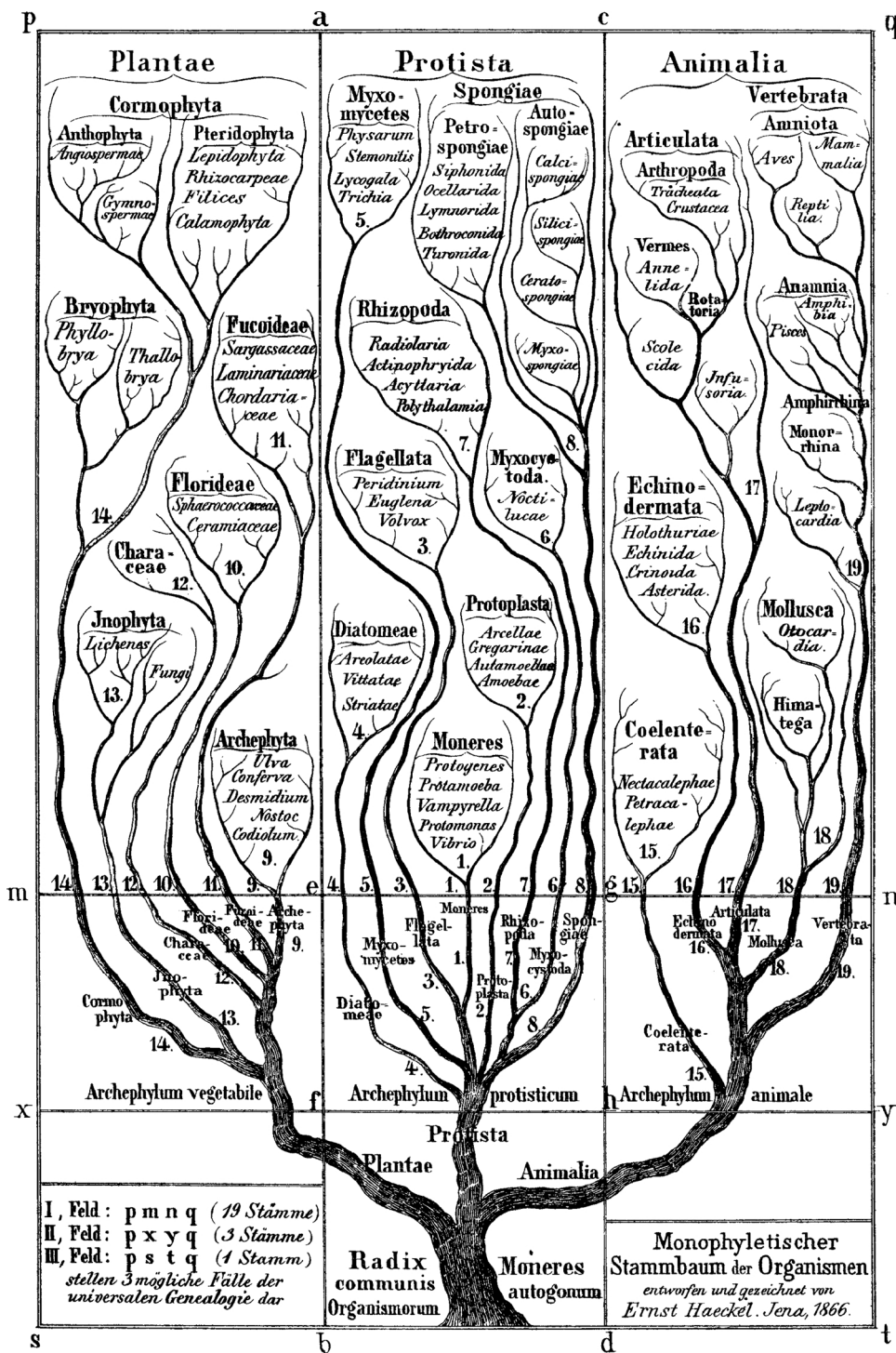


Fig. 1. Haeckel's (1866) scala naturae. The left and right branches of this "tree of life" continued to be refined over the years, especially with the acceptance of DNA sequencing as a central determinant. The microbes—here called *Protista*—were always in contention, however, as was the primitive "protoplasm", the progenotes—here called *Monera*—from which they evolved. (Figure in public domain.) Of such models Darwin (1859) said, "I believe this simile largely speaks the truth" (30), and extended the metaphor by matching buds, twigs, limbs and arborizations to features of the kingdoms of life.

complexity of mammalian cells) and eukaryotes (which contained potentialities for highly differentiated multicellular organisms). But there was growing evidence that modern eukaryotes were themselves that strange kind of hybrid called symbionts, with early eukaryotes incorporating bacteria whose flagella would move them about, or move fluids within them about; mitochondria that would give them energy and other resources; and chloroplasts that would convert solar energy. These "saltations"—quantum jumps in complexity and genetic diversity—were no part of the vision of the New Synthesis. Microbes are profligate, sleeping around with others that were not part of their "species", and undergoing thereby quantal changes in fitness; their

presence and abundance in the world is a triumph of non-Darwinian<sup>8</sup> evolution priming the variability pumps for eventual selection by fitness.

<sup>8</sup> More precisely, "non-Modern-Synthesis", as Darwin's evolutionary theory was comfortable with variation, however acquired (viz., through Natural Selection or wholesale incorporation of other genes and organisms), and whatever the mechanisms (acquired or selected for). To call a theory "non-Darwinian" does not imply that selection (and retention) is not important; it asserts that there are other factors, such as genetic drift (the "neutral theory") that play an important, even often crucial, role. Variation and retention often occur without selection for that gene. Contemporary syntheses which embrace all these factors, and others such as niche construction, culture, and epigenetics (e.g., *Dual Inheritance Theory* and the *Extended Synthesis*) are briefly discussed below. See also (Aldrich et al., 2008).

### 3.1. Lateral gene transfer

A bacterium of one type can acquire genes from another unrelated organism by uptake of bits of their DNA from the environment (“transformation”; governed by about 40 genes in bacteria), by viral infections (“transduction”; perhaps an accidental miscarriage of viral transcriptions), and by direct cell-to-cell contact (“conjugation”; plasmids, strings of DNA that replicate but are not incorporated into the bacteria’s DNA). At least 80% of the genes in each of 181 prokaryotic genomes studied by Dagan et al. (2008) were involved in lateral gene transfer at some point in their history. Clearly the attempt to generate a phylogenetically based taxonomy, to talk in terms of species, is undone by this ability of bacteria to be constituted of some of the DNA of other kinds of microbes, and to be so reconstituted on a regular basis. Lateral gene transfer—profligate incorporation of DNA, exchanging body fluids with anything a microbe fancied—is why resistance to antibiotics can spread so quickly among germs. Not only does this come to the bacterium’s rescue when challenged, such transfer prepares them in advance for challenges from antibiotics that had been used against other microbes, but had never been used against their strain (p. 139). Multiple drug resistance skulked into the hospital. Lateral transfers were in fact saltations—changes to the genetic code that the varieties of bacteria had not slowly acquired through variation and selection, but rather through random but not infrequent gene transfer. Some survived and were passed on, exemplifying the inheritance of acquired characteristics. Eventually some may have contributed to fitness and multiplied,—a blend of Lamarckian evolutionary processes that jump-started new strains, followed by Darwinian selection to amplify the presence of the successful ones thereafter. This intimacy in progenitor microbes might even explain the universality of the genetic code itself: the same double helix with the same bases and the astonishingly high similarity of its structure in creatures as phenotypically diverse as humans, slime molds, and liverworts.

### 3.2. Vertical, horizontal, crossing

In addition to the vertical transfer of genes from parent to daughter cells, or to offspring in eukaryotes, there is also the horizontal—lateral—transfer of genes in microbes. The former leads to the species shown in the left and right columns of Fig. 1. The latter leads to trees of life with many crossed (fusing) branches. This *reticulate* evolutionary pattern in bacteria thwarts construction of, and meaningfulness of, the typical cladograms shown on the side panels. Since tracing evolutionary paths is deeply problematic (and that was a purpose of such taxonomies), the alternate approach of numerical taxonomy (*phenetics*; emphasizing phenotypic similarity) that avoided speculation about evolutionary paths arose. It was essentially a sophisticated, computerized version of Bergey’s manual; its critics (such as Mayr) claimed it committed the same errors, but in more sophisticated ways. But the other *raison d’être* for such taxonomies was the need for a coherent, systematic way of talking about organisms and their similarities. Absent hope of a secure evolutionary taxonomy, phenetics became the most popular approach to microbiology taxonomy upon its introduction in the 1960’s. There is a possible parallel here for behaviorists, with the methodological variety (akin to the pheneticists with their multi-dimensional metrics of similarity) preferring to consider only data that were secured by public observation (allowing no inferred mental [evolutionary] paths), *versus* the radical variety allowing inferred events—of uncertain causal status and observable only subjectively—because of their phenomenal obviousness and cogency. Radical behaviorists trace the evolution of a stimulus through a private event (e.g., covert verbal behavior) and thence into a response; such non-public machinery comprises their latent variables.

Some bacteriologists suggested that it was “best to think of bacteria as constituting one gene pool from which any ‘species’ may draw genes as these are required...whilst the phylogenetic tree is a reasonable

representation of eukaryotic species [the outer columns of Fig. 1], a reticulated network would be required to represent the evolution of the genome of a bacterial species” (142). But others pursued the search for evolutionary tell-tales, and found some in the most conserved structures in organisms. The machinery that translates the (redundant) codons of DNA into proteins—the ribosomal RNA—is fundamental. If one tinkers with that translation, all the proteins that depended on the former codebook are at jeopardy; rRNA is thus highly conserved. The redundancy of the coding provides both a safety net, and room for some variation in coding maps. rRNA has come to be used, therefore, to estimate the rate of species divergence. A leader in this work is Carl Woese, whose group slowly convinced their colleagues of the existence and reality of an additional kingdom, that they called the *archaeobacteria* (now, the *archaea*). These forms were rudimentary and often inhabited extreme environments, such as salt lakes, boiling springs, and the acid environments of mine runoffs with pHs down to 0. Some abide in the human gut, aiding digestion by converting carbon dioxide into methane; others constitute a substantial portion of the biomass of the oceans. They have both prokaryotic and eukaryotic features. It is currently speculated that they are a transitional form between the earliest prokaryotes, and the eukaryotes living in the outer columns of Fig. 1.

Sapp (2009) tells a fascinating story of ensuing microbiological developments, and Woese’s key role in them. Our own story here must leave it—but encourages interested readers to seek out Sapp’s book; or Woese (2004); or enjoy Woese and colleague’s thumbnail (Goldenfeld and Woese, 2017), from which I excerpt a few words: “a defining characteristic of life is the strong dependency on flux from the environment, be it energy-giving, chemical-giving, metabolism giving, or genetically-giving...with microbes absorbing and discarding genes as needed in response to their environment....Early life must have evolved in an inherently Lamarckian way, with vertical descent marginalized by horizontal gene transfer.” The authors close by quoting Lavoisier: “...we cannot improve ...a science, without improving the language or nomenclature which belongs to it”; concluding: “Biology is about to meet this challenge”. Is behavioral psychology?

## 4. Selection by consequences

“Selection by consequences ... first recognized in natural selection, also accounts for the shaping and maintenance of the behavior of the individual and the evolution of cultures. In all three of these fields, it replaces explanations based on the [efficient] causal modes of classical mechanics” ((Skinner, 1985, p. 501). Skinner’s insight is a modern reflection of *universal Darwinism* (Campbell, 1975; with interesting histories and extensions found in Cziko, 1997; and Plotkin, 1997). This is a compelling vision: Vary-select-retain appears an indomitable account of life. But how much of the behavior of individuals and cultures does it really account for; to what extent can it replace causal modes?<sup>9</sup> We have seen that for the majority of time life existed on earth, and for the majority of organisms now living, small though they may be, vertical selection—selection by consequences—plays a real, important, but restricted role in their evolution. “Darwinian (positive) selection is important but is only one of several fundamental forces of evolution, and not necessarily the dominant one. Neutral processes constrained by purifying selection dominate evolution” (Koonin, 2009, Table 1). Such purifying selection is a life or death matter for the particular organism that gets purified; but those that survived the harrow told everyone else, sister or not, con-“specific” or not, how to do it, and those learned the tricks vicariously, on the original world-wide web. Microbes may not have empathy, but they cannot stop tweeting what they just learned. In eukaryotes, retrotransposons—jumping genes—not only

<sup>9</sup> I take “accounts for” and “replaces explanations based on causal modes” to mean “provides a complete account of, making efficient causes unnecessary”. A reviewer vehemently disagreed; I am nonplussed, and let you the reader interpret the master.

jump within the genome of individual organisms, they can jump between species. The BovB gene that constitutes 25% of the genetic material of cows originated in snakes, and is present in more than 60 other animals (Ivancevic et al., 2017). The percentage coverage is substantially greater if one includes fragments of the transposable elements (TEs) in the count. The L1 TE is found in over 400 species. The Trees of Life drawn by these authors look very different from those shown in Fig. 1. Ivancevic and associates observe that, “Given that these TEs make up nearly half of the genome sequence in today’s mammals, our results provide the first evidence that horizontal transfer can have drastic and long-term effects on the new host genomes. This revolutionizes our perception of genome evolution to consider external factors, such as the natural introduction of foreign DNA.” While recognizing the role of natural selection in all such processes, it is not clear to me how that can provide a complete “account” of such powerful, communal, evolutionary processes.

## 5. The behavior of the organism

As with species, there is no question of the importance of “vertical”—teleological—selection in the behavior of individuals. The behavioral process of shaping is explicitly selectionist, with some forms closely emulating the selection of individuals from populations (Lane, 1964; Platt, 1973; Galbicka, 1994). What happens after you do it, whatever it is, matters. But how much? How large a role does such selection play? After a salient event you may promise yourself that you will never do it again; or that you must do it more; but do you? In days when my heart was harder, I trained monkeys to press a lever the only consequence of which was to periodically deliver a painful electric shock—not to me, but to themselves. (This requires that they be shaped to lever-press first, either by a schedule of positive reinforcement (Kelleher and Morse, 1968), or one of shock avoidance.) The monkeys continued this masochistic behavior until I had just enough data; I pulled the plug and promised them that I would not do it again.<sup>10</sup> Like (?) the monkeys, there are human cutters who inflict pain on themselves; we can tell stories about negative reinforcement, escaping from self-hatred or numbness, but those are stories. It is not clear how we as behaviorists pull the plug for them. We are more successful with self-injurious behaviors of the autistic spectrum disorder; but it is working uphill against a perverse Law of Effect (perverse, unless we rebadge everything that maintains behavior as a reinforcer, trading prediction for post-hoc consistency).

### 5.1. Elements

A qualification of the teleological Law of Effect was first offered by its father. E. L. Thorndike noted that in addition to contiguity with satisfiers, responses became associated to context more or less readily depending on the animal’s set (drive state, fatigue, etc.) and the belongingness of the response and potential reinforcer to that state (Thorndike, 1935). When a predator at leisure catches sight of a prey, its state may change, with an associated set of reflexes prepared for discerning, tracking, chasing, pouncing, and dispatching. Timberlake took this observation a step further by ensconcing it in the ethograms of animal behaviorists, generating a behavior systems theory<sup>11</sup> (Timberlake, 1993, 2001; see Killeen, 2014 for an overview and implementation). When engaged in a component of a behavioral state such as predation, each successive step toward the goal enhanced the probability of some actions, and inhibited the probability of others.

<sup>10</sup> I didn’t. Our research sufficed to show that the period of safety after a shock was a negative reinforcer that maintained the lever-pressing (cf. Himeline, 1970).

<sup>11</sup> Compare with the systems biology discussed below. Skinnerian behaviorists also recognize control by context, calling it “the discriminated operant”; but key issue here is the treatment of the context as a releasing—or dispositioning—mechanism for behavior, a step which few behaviorists took (but see, e.g., Holland, 1992; Jenkins et al., 1978).

Thompson (2007) proposed that an organism’s integrated repertoire of operant behavior constitutes a biological system, and emphasized the importance of understanding how elements in that system play roles in other biological systems. Just as genes are exchanged and recombine in prokaryotes, Thompson and Lubinski (1986) identified response classes that might serve as elementary units, and speculated on how they might interact and recombine for novel arrangements of actions. Balsam and colleagues have analyzed the component elements of lever-pressing, pecking, and human learning of novel movements (Stokes and Balsam, 1991; Balsam et al., 1992; Balsam et al., 1998).

Baum (2012) has emphasized the induction of behavior by its context, while also endorsing the multilevel nature of behavior selection (Baum, 2016). Even in a simple experimental enclosure, Pellón and Killeen (2015) demonstrated competition and facilitation among induced responses. Just as the embryo develops as a heritage video of some of the stages through which we have evolved (pp. 32, 33), the misbehaviors and non-optimalities of operant repertoires are echoes of the natural appetitive and defensive repertoires which behaviorists attempt to select—shape—to our ends in the laboratory. Thus, many contributors to the behavioral literature have recognized the importance of dealing with the interaction of functional units, but little in the way of a coherent theoretical approach has emerged (with the interesting exception, perhaps, of Epstein’s generativity theory: Epstein et al., 2013; Epstein 2014, 2015). Whereas selection by consequences plays a role in fine-tuning instrumental actions in all of these accounts, many other forces of lateral interactions among the elements are shown in these references to be at work. The origins and machinery of variation and competition is slowly becoming an important part of behavioral analysis.

Many behaviorists have questioned the role of contingency—in particular reinforcement—in behavior analysis. Some have wondered if it was all we needed (Timberlake, 2004), others wondered if we needed it at all. Davison and colleagues (Davison and Baum, 2006; Cowie and Davison, 2016; Davison, 2017) suggest that the efficacy of conditioned reinforcers (and perhaps even primary reinforcers) is due to their signaling ability—telling the animal what to do the next time it is in that situation. Shahan (2017, 2010) comes to similar, guarded, conclusions. Killeen (2014) proposed a hybrid theory, with reinforcement consisting of the transition between Timberlakeian modes and modules (cf. Baum, 1974). Such reinforcement fine-tunes the location, timing and topography of the perceptual or motor acts that were proximal to the transition. The class of acts available for reinforcement depends on their belongingness in that module. Killeen and Jacobs (2016, 2017) went further, treating the “three-term contingency” as a specification of states: the stimuli that are operative at any moment, the responses that are engaged, and the consequential stimulus called a reinforcer. To these they added the motivational state of the organism *O*, which tunes the other three elements. All these things we infer, with error, from measured behavior: Error in ascribing the operative stimulus at any moment is due to vicissitudes of attention; in specification of the response to our abstraction of gross motor acts into the activation of a switch; in efficacy of the reinforcer to context and satiation. The 4-term “contingency” model  $O: S_D-R-R_C$  stands in for a kind of filter that we impose on an extended stream of behavior to infer those states from data, with error, and from which we may then predict ensuing responses (ParticleFilter, 2017); or attempt to arrange those states to control behavior. Perhaps the animal itself may come to be characterized as such a filter (Cowie et al., 2013; Davison, 2017; McDowell, 2017). Selection by consequences plays a role, but there are other important players; by itself, consequential reinforcement cannot adequately account for behavior.

## 6. The evolution of cultures

Skirt lengths go up or down, tattoos on or off, standards for politicians strict or lax. Positions on these issues may be reinforced or

punished, but as Skinner noted, consequences cannot account for the first occasion of a response. Oftentimes one only gets to make the first response: Tattoos are tough to erase. Join the military, and war may leave you no choice to re-up or refuse. A baby is a 20-year commitment; marriage is “till death we do part”. First times count, and selection by consequences cannot account for them. There are causes, of course, and individuals often try to infer them when asked for reasons. There may be familial or social pressure, but that is no part of selection by consequences. Once engaged, reinforcers arise; tattoos tag groups or attitudes, adding cohesion and mutual admiration (Henrich and McElreath, 2007; McElreath et al., 2003); the mutual support in elements of a platoon is a crucial part of war (Keegan et al., 1985); marriage is a cauldron of reinforcement. But these often function at a level of making the relationships endure—not recruiting new tattoo bearers, or new wars, or another partner in the relation. Reinforcement operates here on a different level. Memes spread through a social contagion that we in the behavioral community do not yet understand. Even scientific categories that organize and simplify often leave a lingering set of biases; memes as implicit Bayesian priors, as it were. The names for epochs of stone-age tool techniques, such as *Mousterian*, may blur, rather than clarify, the relationship between early *Homo* species (e.g., Shea, 2014).

Media magnifies the impact of opinion leaders. When the rapper B.o.B tweeted about the Flat Earth Conspiracy, Google lookups for “Flat earth” trebled. When NBA player Kyle Irving said “the earth is flat” in a podcast a year later, they more than doubled (<https://tinyurl.com/y7d3mhy8>). The retweeting of strong opinions may have played an important role in recent elections. How does such powerful horizontal transfer of memes fit into the framework of the three-term contingency?

“Microbial behavior must be understood as predominantly cooperative” (Goldenfeld and Woese, 2017). Yet in eukaryotes the Darwinian competitive struggle is the main engine of evolution. Which kind of beast is a culture? Must we seek hidden reinforcers for random acts of kindness? Jones and Rachlin (2006) demonstrated smooth generalization gradients of generosity across the dimension of perceived social distance. These could be hard to explain with selection by consequences. One might argue that social proximity indicates genetic relatedness, and what we see is a normal generalization gradient along this dimension. If so, it is an amazing demonstration of kin-selection controlling economic behavior to a fine point. Furthermore, it resonates with the inverse-square decline in emotional involvement as a function of distance to other cities in which a calamity befalls the population (Ekman and Bratfisch, 1965; Lundberg et al., 1972), in which case kinship is an implausible explanation. Labeling these as generalization gradients does not explain the empathic and emotional involvement across social and physical distance; nor is it clear how selection by consequences can account for them.

It is obvious that much of the instigation of behavior in humans is through lateral transfer of memes. We do what others in our reference group do. The survival of cultures is largely indifferent to most such transfers; tattoos don’t make for more or less successful cultures (Diamond, 1997), nor do musical hit parades; although in extrema, habits sometimes do (Diamond, 2005): look no farther than the Shakers (and their antitheses in Catholic and Mormon communities). The concept of selection by consequences in cultures is problematic: Group selection requires much more intense intergroup selection pressures than intragroup pressures to shift the population. No doubt we correctly perceive some cultures to be much more successful than others—contrast Benelux with Somalia. How much selection by consequences has to do with that is another matter.

### 6.1. *Mimetics*

*Mimetics* concerns imitation; the things imitated are memes, and include not only ideas but also emotions. A small insight into how the world became deranged eighty years ago can be obtained from scenes in *Triumph of the Will*, available on *YouTube*. Pure induction,

consequences be damned. Consequences followed, of course, as properties were confiscated, nonconformists punished, conformists rewarded, and the world burned. But the righteous ardor of populist movements is not well explained as instrumental behavior, at least in the eyes of this observer. The types of lateral gene transfer are superficially mimicked by lateral meme transfers: 1. *Transfer* of genes from the environment: print media. 2. *Transduction* of RNA by virus: social media. 3. *Conjugation*: personal instruction. But the importance of the topic demands a serious study of the functional nature of memes. An important step in that direction was taken by Cavalli-Sforza and Feldman (1981; and by the more heterogeneous group of *memeticists*). Inter alia, these authors distinguished cultural habits by whether the strongest influence on them was vertical or horizontal. We “inherit” from our parents our religion and politics almost as surely as we inherit our height—vertical transfer of memes. We absorb our dances, jargon, and dress from our peers—lateral transfer. Why these anisotropies in the “reticular network” of influence?

Memes are units of cultural contagion and evolution—from smiley faces and “Have a nice day”, to “Not a problem” for requests well-within the server’s job description. More importantly, memes are part of survival skills such as flint knapping and street crossing. Memes are unlike genes because, with the relatively rare exception of mutations, genes do not change between generations, even though their prevalence does. Memes are recreated by each generation, as echoes of utterances, or as attitudes, or as learned skills. They blend with the other knowledge or ability in each generation, and are changed as they pass. They diffuse horizontally among cultures (Tostevin, 2000). Simple models of such diffusion account for cultural changes such as baby name popularity (Hahn and Bentley, 2003; Acerbi et al., 2012). Memes often evolve faster than the bodies that host them, and contribute to, or detract from, the fitness of those bodies. The bodies swim or sink in that culture, as they can advantage themselves of it or not. Memes and other rules often trump contingency-shaped behavior, making such behavior insensitive to consequences (e.g., Fox and Kyonka, 2017).

It is clear now that our bodies have never been single organisms: “A diversity of symbionts are both present and functional in completing metabolic pathways and serving other physiological functions. ...Animal development is incomplete without symbionts. Symbionts also constitute a second mode of genetic inheritance... The immune system also develops, in part, in dialogue with symbionts and thereby functions as a mechanism for integrating microbes into the animal-cell community. Recognizing the ‘holobiont’—the multicellular eukaryote plus its colonies of persistent symbionts—as a critically important unit of anatomy, development, physiology, immunology, and evolution opens up new investigative avenues and conceptually challenges the ways in which the biological subdisciplines have heretofore characterized living entities” (Gilbert et al., 2012, 325). How might we incorporate this more holistic approach into the analysis of the behavior of organisms and their cultures, both those that compose them and those that they compose?

There are many valuable but still-undigested ideas in systems biology, dual inheritance theory, and the extended evolutionary synthesis that may be plumbed in that endeavor. Those systems and theories and syntheses are still more goals than accomplishments. For that, they give elbow room for behaviorists hoping to exploit the many valuable insights found in these literatures. As one student of the co-evolution of society and nature put it, “most theories about more complex phenomena are underdetermined by our observations and over-determined by the ideas that we bring to bear on them” (van der Leeuw, 2004, 121). Here models—mathematical and computational—help reduce the ideas to parsimonious maps of data, and from those induce well-grounded theories. It is in systems biology that we find computational models most thoroughly exploited (*SystemsBiology*, 2017). In behavior, McDowell’s work comes closest to this view (e.g., McDowell and Caron, 2007; McDowell and Popa, 2010; McDowell, 2017). Systems biology attempts, after reductionist analyses, to move forward to a

synthetic integration, often involving dynamic systems analysis and synergetics. Cultural patterns can be self-sustaining emergent structures. This anti-neoDarwinian view sees the genome as an ‘organ of the cell’ (Barbara McClintock, 1984, quoted in Noble, 2015; cf. Jablonka and Lamb, 2007), embedded in, and playing a central, but not dominating role; it is a view of interacting systems, with the potential for ‘downward causation’, not unlike that argued for by Sperry (1969) in his analysis of the role of conscious processes in the control of behavior.

Dual inheritance theory (DIT) treats the coevolution of genes and cultures. Richard Wrangham (2009), for instance, has argued that cooking made us human: We could not generate enough calories for our energetically expensive brain until we learned how to break down raw foods with heat; and once we turned that critical point, our teeth and gut became smaller, our brains larger, our sexual dimorphism greater, and our social organization more complex. DIT gains strength from the interplay of keen observation leveraged by the effective use of mathematical models (e.g., Boyd and Richerson, 1996). Experimentation can also play a role: Morgan and associates (Morgan et al., 2015) used five different ways of teaching flint knapping to subjects, ranging from none or simple imitation to gestural or verbal instruction. The probability of a hit yielding a successful flake was more than threefold greater in the verbally instructed over the uninstructed. But, as with memes, by the fifth generation of transmission of this information from one generation to the next, the performances among lineages no longer differed. The teaching must be reinforced with practice to remain effective—a nice symbiosis of rule-governed and contingency-shaped behavior, of “knowing that” facilitating “knowing how”, with the latter keeping the former accurate. The authors argued that “hominin reliance on stone tool-making generated selection for teaching and language” once the brain had evolved to the point of supporting it; the prior long (700,000 years) relative stasis in evolution of stone tools may have been for want of speech. The place to start to understand DIT is the book by Richerson and Boyd (2005). An excellent analysis of the biases that sway such cultural transmission is found in the exposition of Henrich and McElreath (2007); a lovely demonstration of how behavioral approaches can inform this literature is found in (Baum et al., 2004).

The extended evolutionary synthesis (e.g., Laland et al., 2017) incorporates Darwinian and Lamarckian selection, multilevel (both group and individual; Baum, 2017) selection, reticulate evolution, fitness landscapes, epigenetics, and niche construction. All of this is already implicit in Darwinian selection; but that is so rich a concept that its implications need to be drawn out. Perhaps the most important message it communicates, like the above variants, is that life takes on characters of its own, self-organizes, finding far-from-equilibrium ways of thwarting the laws of thermodynamics, a seminal vision of Schrödinger’s (1943), developed by Prigogine (Prigogine and Stengers, 1984), and most thoroughly exploited in this subfield. Behavioral research can learn from, and in turn inform, these various extensions and reinterpretations of Darwinian evolution.

## 7. Conclusion

There can be no conclusion: The field of genetics is moving so quickly it would make any obsolete before it reached print. Science outpaces its fiction. *Synthetic Genomics, Inc.*, Craig Venter’s company, has designed and synthesized a minimal bacterial genome. The company can sequence the genome of any organism, transmit it electronically, and is now building robots to reconstitute it; thus, the title of his recent book, *Life at the Speed of Light* (Venter, 2013). Theoretical adjustment proceeds more slowly than its technology; read Sapp (2009) to understand how contentious every step forward in microbiology had been, and how provisional each insight was in its time. The data were seldom ignored or dismissed, but always subject to reinterpretation. We in the behavioral community face similar interpretive challenges: How to model behavior in empirically based ways that place it ever more securely in its larger evolutionary and social context.

In 1963 Verne Grant published *The Origins of Adaptation*. It was a study of neo-Darwinian population biology securely based on a large compass of the literature, set in a broad cosmic context (p. 110; to appreciate this, you must free yourself from the meme that *evolution* means *Darwinian*). Grant described various stages of evolution, the first being the atomic evolution some 14 billion years ago when matter condensed from the singularity. The second occurred about 4 billion years ago, when the elements evolved into carbon compounds and others of greater atomic weight. Soon thereafter planets cooled enough to let life emerge as self-reproducing virus-like naked genes. Protoplasm was on the scene. In a cosmic blink, organic (Lamarckian) evolution predominated, shaping the air and environment (de la Cruz and Davies, 2000). Many millions of years later Darwinian evolution of species began. About a million years ago a motley array of apes slipped through Darwin’s filter, and with their halting progress toward speech, cultural evolution arose. We are now arrived in the Anthropocene with the invasive species *Homo sapiens* overwhelming local Darwinian evolution through cultures of domination (Ceballos et al., 2017). Although evolution continues in *Homo sapiens*, it is no longer through inter-specific competition.<sup>12</sup>

In an ironic twist, the very machinery by which prokaryotes had incorporated genetic information from peers has been mastered by the eukaryotic ape. Prokaryotes place foreign DNA, letters from friends, into their genome as maps of what to defend against. They flag it on either side with clustered, regularly interspersed, short palindromic repeats (CRISPR) of DNA. Long sequences of these constitute a library of enemies defeated. If one such finds its way into the organism, the CRISPR proteins of the bacteria and archaea recognize and destroy it by cutting it out. Microbiologists have invented ways to guide these scissors to precise targets on the chromosome, to excise particular sequences. In further irony, viruses are often used as the delivery device. Mice have been successfully treated for muscular dystrophies with CRISPR-Cas9 gene editing, which has been used in more than 3 dozen species. Experimentation with humans is beginning. The  $\beta$ -thalassaemia mutant has recently been corrected in human embryos (Liang et al., 2017). Antiviral and anti-cancer therapies are being developed in translational research labs. CRISPR hobby kits are available (<http://www.the-odin.com/>), filling the roles of the chemistry sets given to children in the 20th century. Winners of high-school science fairs are using the technology (e.g., <https://goo.gl/naxA3C>). An invaluable guide to the technology and its ethical implications is found in *A Crack in Creation* (Doudna and Sternberg, 2017). The Book of Life is being spell-checked; it will not be long before the copy-editors will try to improve its prose.<sup>13</sup> This is already happening in livestock: In the first 5 years of this decade more than 300 differently edited pigs, cattle, sheep, and goats were produced in efforts to improve commercial traits (Tan et al., 2016). A decade ago—ages in this rapidly evolving culture—Freeman Dyson observed that: “Cultural evolution has replaced biological evolution as the main driving force of change. ...As *Homo sapiens* domesticates the new biotechnology, we are reviving the ancient pre-Darwinian practice of horizontal gene transfer, moving genes easily from microbes to plants and animals, blurring the boundaries between species. We are moving rapidly into the post-Darwinian era, when... the rules of Open Source sharing will be extended from the exchange of software to the exchange of genes” (Dyson, 2007). Evolution, itself, evolves (Noble et al., 2014).

<sup>12</sup> The leading causes of death in rich countries strike after child-rearing ages; the leading causes in poor countries are infectious diseases, taken in *toto*.

<sup>13</sup> A 2015 Asilomar Conference proposed a moratorium on the use of CRISPR/Cas9 technology to modify human germlines, a use that then appeared to be in the distant future. One of the obstacles to its proximal deployment had been the error-prone nature of such editing. But that obstacle has just been overcome by a student in Doudna’s laboratory (Grens, 2017). As one scientist asked, “Would it not be unethical not to fix something if you could?” (Sheridan, 2015). For a review of the strengths, weakness, and ethics of this moratorium, see (Guttinger, 2017).

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