CHAPTER 2

THE EVOLUTION OF THE SYMBOLIC SCIENCES

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From biological to symbolic evolution

How human symbolic evolution is studied depends upon how humans, evolution, and symbolism are defined, and these definitions change according to advances made in scholarly research. The term *human* is traditionally associated with our species, *Homo sapiens*, although it can refer to any of the numerous species that are classified under the *Homo* genus (Tattersall, this volume). *Symbolism* is a concept that used to straightforwardly refer to notational marks such as icons, indexes, or symbols. The search for symbolism within the diverse *Homo* lineage, however, has additionally come to refer to visible and tangible tokens, cognitive and behavioral traits, individual and group phenomena, and material and technological extensions thereof (Majkick, this volume; Nowell, this volume). *Evolution* has for many years been defined in Darwinian and selectionist terms, but today, evolutionary biologists are actively engaged in expanding upon the tenets, scope, and applications of the standard evolutionary paradigm (Gontier, this volume). This expansion toward other evolutionary theories now influences research on the rise of human symbolism.

This chapter focuses on the evolutionary aspects of human symbolism, and it provides a scientific-philosophical and science-anthropological analysis of the intellectual background and structure that underlies past and current theorizing on symbolic evolution. It investigates how early disciplines such as traditional evolutionary epistemology, communication studies, biosemiotics, and sociobiology originated by systematically implementing theoretical aspects of biological micro-, meso-, and macroevolutionary schools into research on human behavior, cognition, language, and sociocultural group formation. Afterwards, it examines how the successful implementation of Neo-Darwinian evolution theory into human behavioral, cognitive, and sociocultural studies has founded new disciplines including evolutionary psychology, evolutionary linguistics, evolutionary archaeology, evolutionary anthropology, evolutionary sociology, and evolutionary economics. The chapter ends by analyzing how these fields are currently helping to expand the classic evolutionary paradigm by implementing important insights from evolutionary developmental biology, ecology, and reticulate evolution studies into the study of human symbolic evolution.

EPISTEMIC ROOTS AND CONTROVERSIES OF THE SYMBOLIC EVOLUTION SCIENCES

The implementation of *Darwinian* evolutionary thinking into the traditional humanities starts in the early decades of the twentieth century, with the rise and cross-fertilization of **evolutionary epistemology**, **communication theory**, and **(bio)semiotics**. These research fields respectively study *knowledge*, *information*, and the *meaning of signs* (Figure 2.1).

Evolutionary epistemology and biosemiotics endorse a *mesoevolutionary* or *organismal* and thus developmentally oriented research outlook that helps to found the schools of **ethology** and **psychology**. These schools extend the scope of the *Modern Synthesis* that until then had more narrowly focused on the evolution of *anatomical form*, by bringing evolutionary research to bear on the study of organismal *behavior* and *cognition*.

Communication studies also expand on the scope of the Modern Synthesis, albeit from within a different direction. Inspired by information and game theory, communication studies commence a *micro-level* study of *information* and how it is transferred by *signals and signs*. The new language introduced by information and communication theory would subsequently become adopted in evolutionary biology by molecular geneticists to describe how genes, through processes of "transcription" and "translation," "encode" for anatomical and behavioral traits, and how these traits are "transmitted" genetically over generations.

Sociobiology arises in the 1970s as a branch of the phylogenetically-oriented discipline of zoology. Sociobiology adopts the terminology associated with information theory and *theoretical population genetics*. The field understands cognition and behavior as information that is genetically "programmed" and transmissible over generations through time. The school therefore endorses the view, typical of the *Neo-Darwinian Synthesis,* that *microevolution* (the genetic part of population genetics) brings forth *macroevolution* (the population part).

From the 1990s onward, sociobiology becomes complemented by **evolutionary psychology,** and from there onward, the new human symbolic evolutionary sciences develop. The new symbolic evolutionary sciences comprise the disciplines of **evolutionary linguistics**, **evolutionary anthropology**, **evolutionary archaeology**, **evolutionary sociology**, and **evolutionary economics** that, as the names imply, each implement an evolutionary outlook into their classic counterparts.

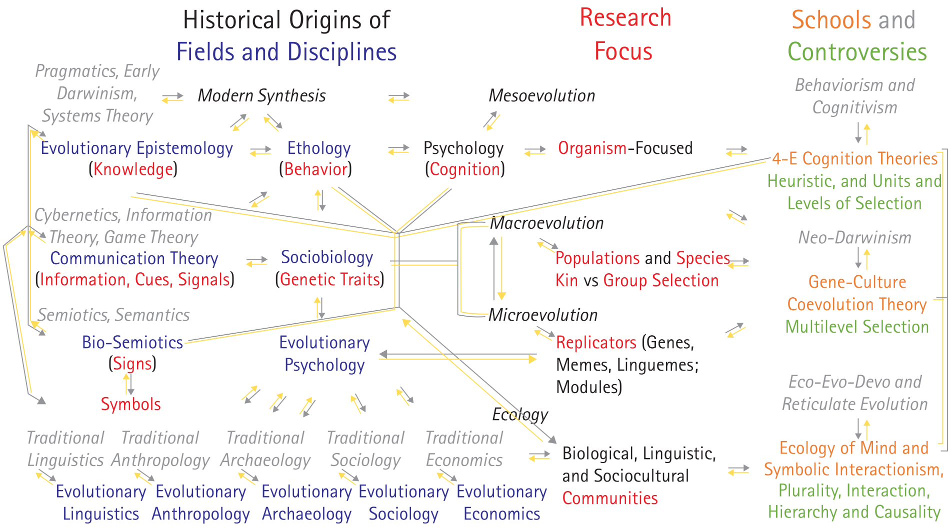

FIGURE 2.1: The structure of the symbolic evolutionary sciences. The concepts are explained in the body of the text where they are marked in bold.

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The symbolic evolutionary sciences originally proceeded by modeling their research outlook to that of evolutionary biologists active either in the micro-, meso-, or macroevolution schools. However, today, the new disciplines are developing somewhat independently both from the biological sciences as well as from the classic symbolic disciplines they once belonged to. In addition, they are steadily integrating insights from *ecological and evolutionary developmental biology* (eco-evo-devo) and, albeit to a lesser extent, *reticulate evolution schools*. In what follows, these fields and disciplines, and the controversies they try to resolve are analyzed in more detail.

THE EVOLUTION OF KNOWLEDGE, BEHAVIOR, AND COGNITION

One way whereby the evolution of symbolism can be studied is by inquiring into the evolution of knowledge, behavior, and cognition. Fields that first systematically study these traits are evolutionary epistemology, ethology, and psychology. **Evolutionary epistemology** (Lorenz, 1941; Popper, 1963; Campbell, 1960, 1974; Bradie, 1986; Wuketits, 2006; Slijepcevic, 2021) is a field within the philosophy of science that arises through a synergy between naturalized epistemology and comparative psychology. "Naturalized" approaches to epistemology reach back to the work of David Hume who understood knowledge as a "psychological phenomenon" (Quine, 1969). "Evolutionary" epistemologists seek out the evolutionary foundations for this knowledge capacity, originally especially by applying Darwinian selection theory to problems studied in philosophy.

Evolutionary epistemologists break with older philosophical traditions that understand knowledge as a mental capacity exclusive to humans. Rather, evolutionary epistemologists recognize **knowledge** to be portrayed by all living **organisms**, and they redefine knowledge in such a way that it includes both **cognition** and **behavior**. Even anatomical form or physiological traits such as breathing, digestion, or the pumping of the heart become understood as nature's way of evolving "inductively acquired knowledge" (Lorenz, 1941; Campbell, 1974). Evolutionary epistemology therefore puts a halt to the controversies between **cognitivism** and **behaviorism** over which has primacy over the other, the mind or the body; and whether or not organisms that lack neurological substrates can demonstrate intelligible behavior. Rather, both anatomy and behavior are understood as cognitive.

The field of **ethology** is a direct outgrowth of evolutionary epistemology. It understands behavioral and cognitive traits as "organs" that evolve by means of natural selection just like anatomical traits do (Lorenz, 1958). This tradition furthermore asks how *teleonomic* or goal-directed behavior can be defined and explained evolutionarily (Pittendrigh, 1958). Answers are found by modeling themselves to evolutionary biologists, and ethologists (Tinbergen, 1963) distinguish between "four causes of behavior" (Table 2.1). From these four causes, the physiological and ontogenetic causes are "proximate" causes that link to ontogenetic and ecological research as it is conceived in the rising *eco-evo-devo paradigm*; while the adaptive and evolutionary causes are "ultimate causes" that link to phylogenetic and *sociobiological* research.

Ethology then further diversifies into "behavioral ecology" (Krebs & Davies, 1978; Alcock, 1979; Borgerhoff Mulder & Schacht, 2012) and "cognitive ethology" (Allen & Bekoff, 1997; Andrews & Beck, 2018). These fields respectively take on the study of animal behavior and cognition.

Evolutionary epistemologists are additionally active in the school of **psychology** that diversifies into behavioral (Skinner, 1938, 1981), child-developmental and cognitive (Piaget, 1970), comparative (Campbell, 1974), primatological (von Glaserfeld, 1974), neurological (Changeux, 1983; Edelman, 1987) and numerous other subdisciplines. These fields are originally set at implementing classic *adaptationist* and **Early Darwinian** views. Under the influence of non-adaptationist evolutionary epistemology that is in turn captivated by early evolutionary developmental biology (evo-devo) as well as **ecological** theories, these fields then transition toward more *constructivist* views on knowledge.

The shift from adaptationist to constructionist accounts can be illustrated as follows. To understand cognition in animals, such as why newborn ducks, for example, instinctively follow the first moving subject they see, Lorenz (1941) redefined Immanuel Kant's "synthetic a priori" claims as ontogenetically a priori (innate) but phylogenetically "a posteriori" (evolved over the course of evolution). In nature, the first moving subject that newborn ducks see is their mother, and it is in the youngsters' best interest

Table 2.1: Causation in Neo-Darwinism and Ethology

Causation according to Mayr (1961), a Neo-Darwinian

Proximate causation	**Ultimate causation**
Problems of physiology and development.	Problems of evolution and adaptation.
How do traits evolve?	*Why* and *for what* do traits evolve?
"The functional biologist is vitally concerned with the operation and interaction of structural elements [. . .]. His ever-repeated question is 'How?' How does something operate, how does it function? . . . [H]is approach is essentially the same as that of the physicist and the chemist."	*"The evolutionary biologist differs in his method [. . .] His basic question is Why?.' [. . .] It may mean 'how come?' but it may also mean the finalistic 'what for?.' It is obvious that the evolutionist has in mind the historical 'how come?' when he asks 'why?'"*

The four causes of behavior in Ethology according to Tinbergen (1963)

For ethologists, behavioral patterns need to be studied like functional organs and these organs require a causal analysis of their "machinery" from the level of "supra-individual societies all the way down to Molecular Biology."

1. **Physiological causation**
   How do genes, proteins, cells, the brain, the body with its hormonal and muscular systems shape behavior?
2. **Adaptive causation (survival value)**
   Adaptationists study the outcome, the functions, or effects of behavior and ask "what" the survival value of a behavior is, i.e., "*what*" is a behavior "*good for.*" What are the costs and benefits of a behavior and how does it help in survival?
3. **Ontogenetic causation**
   How does the functional behavior develop during the course of an organism's lifespan (developmental causes), and *how* does the environment change the behavior (environmental causes)?
4. **Evolutionary causation**
   Why did the behavioral trait evolve in the way that it did? Natural selection is not necessarily the cause of the origin of the behavior. Physiological or ontogenetic causation might underlie the behavior and this behavior can then possibly become favored via natural selection.

For a discussion, see Gontier, N. (2012). Applied evolutionary epistemology: A new methodology to enhance interdisciplinary research between the human and natural sciences. *Kairos 1*(4), 7–4; Gontier, N. (2021). Hierarchies, networks, and causality: The applied evolutionary epistemological approach. *Journal for General Philosophy of Science 52*, 313–334.

to follow her around. Lorenz suggested that such imprinting behavior or other inborn expectations that organisms have about the world are an outcome of evolution and more specifically of selection. In this sense, organisms as well as the behavior and cognition they portray, become understood as evolved theories or "conjectures and refutations" (Popper, 1963) about the environment, or as nature's way of "learning by trial and error" (Skinner, 1981; Riedl, 1984). Another example is the following. If fish are able to survive and reproduce in water, then, the scholars reason, their bodies must be adapted to this environment, and they can thus be understood as evolved and unfalsified theories of the water (Popper, 1972; Munz, 1993).

Such views, however, can only work under the assumption that organisms actually adapt to (the features of) their environment through natural selection. These adaptationist views, however, are now considered naïve and they are moderated by more constructivist views. Organisms are on the one hand genetically constrained in how they can evolve and adapt to a certain environment, and on the other hand, they can also alter their environmental settings. Through their behavior, organisms can construct their niches "ecologically" (Lewontin, 2000), "socioculturally" (Laland et al., 1995), and "cognitively" (von Glaserfeld, 1995; Magnani, 2017). That means that organisms do not so much adapt to an outer world as that they actually shape and rebuild their environment until it becomes hospitable (Gontier, 2018a). Fish, for example, do not construct the water of the rivers or the oceans, but they can nonetheless alter its composition (by, for example, changing the pH level). Beavers can build dams and construct a niche that is different from the vast aqueous environment they are part of. Or humans can form mental constructs about an outer world that do not match with reality but that nonetheless enhance their survival.

The physiological or ecological expectations that organisms have, including mental images or ideas they might have of the environment, are now recognized to result from active constructions. A constructivist stance implies a transition from a "dual" perspective on how organisms relate to their environment, one where organisms are understood as being passively selected to fit the environment, to a more "dialectical" perspective where they are recognized to construct their environment (Levins & Lewontin, 1987). Such active construction can already be understood as a form of symbolization.

In constructivism, furthermore, lie the roots of **4-E cognition** (Rowlands, 2010; Newen et al., 2018; Figure 2.2) that currently underlies theorizing in psychology. 4-E cognition theory understands cognition as embodied, embedded, extended, and enacted. Cognition is embodied in organismal physiology and everyday behavioral activity (Maturana, 1970; Varela et al., 1991). It is embedded or grounded (Barsalou,

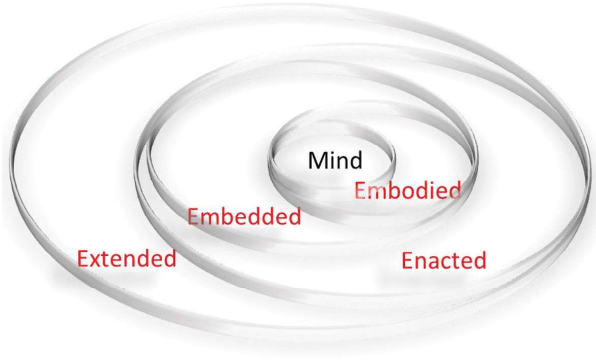

FIGURE 2.2: 4-E Cognition Theory.

Source: © Nathalie Gontier

2008) in sociocultural and environmental ecologies that provide affordances and constraints to how cognition develops (Gibson, 1977). Cognition is extended into material and technological artifacts (McLuhan, 1964; Clark & Chalmers, 1998) that underlie the formation of new ecologies or niches. And cognition is enacted, which means that cognition is brought forth by the phenomenological, lived experiences or actions of a subject (Noë, 2004; De Jaegher & Di Paolo, 2007; Ye et al., 2019).

Adherents of 4-E approaches to cognition counter older Cartesian and representational approaches to cognition that draw barriers between the organism and its environment on a *macro*-level, the organism and its body on a *meso*-level, and the organism and its various mental representations on a *micro*-level. Such barriers require a "central processor" or "language of thought" (Fodor, 1975, 1981) that performs some kind of "computation" or "translation" from, for example, (sensorimotor) perception to concept (mental image or idea), to language. This language of thought is then hypothesized to be materialized on a *micro-level* into inborn "brain modules" that enable the acquisition and processing of language, numerical sense, and other mental capacities (Fodor, 1983).

Contrary to these views, 4-E cognitive scientists aver for a more dynamic understanding of "brain-body-environment systems" (Beer, 2008; Varela et al., 1991). Cognition here becomes centralized, not in brain modules at a *micro-level*, but in the individual organism at a *meso-level*. The organism, in this view, is characterized as self-regulating and self-organizing or "autopoietic" (Maturana & Varela, 1980), which is why cognition is understood as enacted. Scholars here too thus aim to transition from a passive to an active understanding of organisms (Gould & Lewontin, 1979; Levins & Lewontin, 1987).

The recognition that not only anatomical form but also behavior and cognition evolve, and that behavior and cognition can become materialized and externalized into constructed ecological, sociocultural, or cognitive niches, calls for a rethink of both **the units and the levels of selection** (Lewontin, 1970; Dawkins, 1976; Brandon, 1982). It induces research on the **heuristic** (Campbell, 1974) of natural selection or how selection theory can be "universalized" (Dawkins, 1983), from the study of anatomical form toward molecular genetic or neural (modular) research on a *micro-level*; behavior and cognition on a *meso-level*; and language, culture, and societal systems on a *macro-level*. In the next section we focus on the latter, how selection theory has become implemented into linguistic and sociocultural systems, and how their units of selection have been conceptualized.

FROM SOCIOCULTURAL SYSTEMS TO TRAITS AND UNITS OF SELECTION

Besides studying individual behavior or cognition, the evolution of symbolism can also be studied by investigating the evolution of cultures, languages, and social groups. The cultural, linguistic, and social sciences, however, have long flirted with biological theory while never really engaging with it. Witness to that is the "natural-artificial divide," first introduced by Jean Jacques Rousseau who distinguished human nature from human society; the "synchronic-diachronic divide" adhered to by linguists such as Ferdinand de Saussure or sociologists such as Talcott Parsons; and the "four-field approach" in anthropology (Hicks, 2013), that divides the field into physical anthropology, ethnology, cultural studies, and archaeology.

Even when these fields first start to recognize our *individual* past as an outcome of heredity and biological evolution, scholars emphasize that language, culture, and society are *collective* phenomena that surpass the individual biological organism and its genetic endowment. Kroeber (1940, p. 19) would in this regard contend that culture differs from biology because the latter analyzes the "vertical transmission" of hereditary organismal traits in time, while the former is characterized by the "horizontal diffusion" of societal ideas or material artifacts in space (Figure 2.3). Language, culture, and societal living are considered as *group* phenomena that are acquired by learning and that cannot be reduced to genetic or organismal traits. Culture consequently becomes understood as "superindividual" or "superorganic" (Kroeber, 1917), and the superorganic is said to generate its own forces. Kroeber (1963, p. 62, s. 112) exemplified this position by arguing that "*[t]he mass or body of culture, the institutions and practices and ideas constituting it, have a persistence and can be conceived as going on their slowly changing way 'above' or outside the societies that support them*."

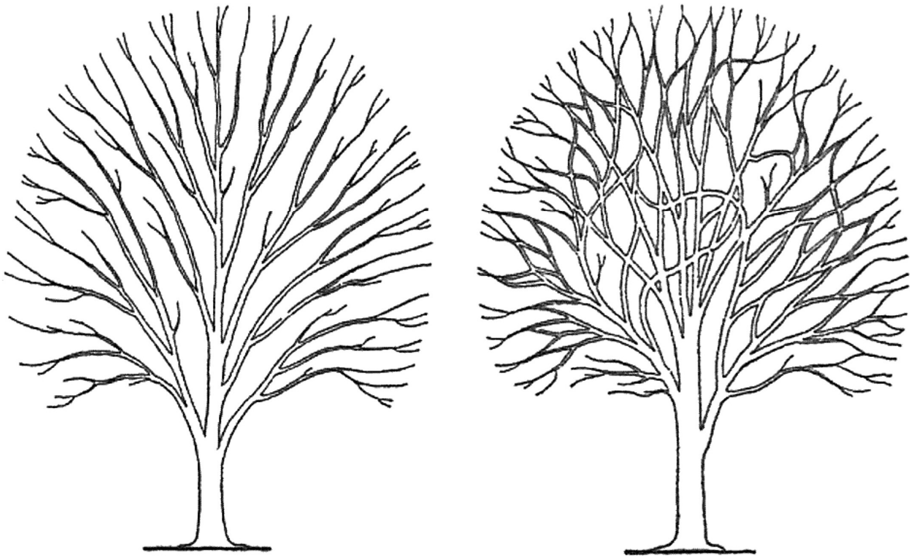

FIGURE 2.3: The tree of life versus the tree of culture according to Kroeber.

Source: Reproduced from Kroeber, A. L. (1963). Anthropology. Hardcourt, NY: Brace Jovanovich. (Originally published 1923), p. 68.

Superorganic, sociocultural phenomena, for Kroeber, surpass the organismal, *mesobiological* phenomena studied by **Early Darwinism** and the **Modern Synthesis**. Today, much of what Kroeber meant by emphasizing the horizontal diffusion of sociocultural ideas and practices can be understood as a form of *reticulate evolution* (Gontier, 2007). But in Kroeber's time, reticulate evolution studies were not integrated into standard evolutionary biological theories.

Instead, with the rise of **Neo-Darwinism**, scholars would on the one hand try to reduce the study of biological form to a *micro-level*, by researching how anatomical form is generated by **genetic traits**, and on the other hand, they would try and expand that study to how genetic traits spread amongst generations of organisms at a **population** and **species** or *macro-level*. These views were then combined by arguing that **microevolution** or change in genetic traits actually brings forth **macroevolution** or group differentiation and speciation (Mayr, 1961). These views would also become adopted by the symbolic and cultural evolution studies.

Implementing Darwinian evolution theory into the sociocultural sciences translates, firstly, into a quest of how and what it is from culture that evolves, and secondly, where culture can be situated within this evolutionary hierarchy. Regarding the first question, how and what evolves, Julian Huxley (1955, p. 3), who gave the Modern Synthesis its name, in an influential paper conceptualized evolution as *both* biological and cultural in kind. He explained his "view of anthropology *sub specie evolutionis*" as a search for "transmissible units" of material culture, language, and social organization. Respected anthropologists and sociologists of his time had called these transmissible units "mentifacts," "artifacts," and "sociofacts" (Gnoli, 2018) (Table 2.2). These facts are not reducible to genetic traits. But just like genetic traits, they come to dissociate from the organisms that evolve them and they tend to be transmitted across generations through time. On these grounds, they can be considered actual units of cultural evolution in general and of selection in particular.

Table 2.2: Units of sociocultural transmission (subject to selection)

Artifacts:

"All physical objects made by man, or man-made modifications of any materials of nature" (Eubank, 1932)

E.g., tools, art

Mentifacts:

"Non-material mental creations which are sufficiently 'crystallized' to be subject to description and analysis, but which are factually separable from their creators" (Eubank, 1932, pp. 356–357); "conceptual symbols" (Bidney, 1953, p. 130)

E.g., language(s), cultural beliefs

Sociofacts:

"Social norms and organization" (Bidney, 1953, p. 130)

E.g., division of labor or moral codes

Huxley's work would thus set in motion a series of debates on what the units of selection are, both in biological as well as in cultural evolution. The **units and levels of selection debate** would later form one of the pinnacles of the 1959 Darwin Centennial where Huxley, at the time president of the British eugenics society (for a discussion see Weindling, 2012), attended the meeting as a guest professor at the University of Chicago. The centennial would be foundational for the rise of the Neo-Darwinian paradigm that then further diversified into the micro-, meso-, and macroevolutionary fields (Smocovitis, 2012; Gontier, this volume).

Regarding the second question of where we can situate culture, this query pertains to how exactly the sociocultural relates to and dissociates from the biological. When analyzed from within a hierarchy, anthropologists, sociologists, and linguists traditionally understand phenomena such as languages, cultures, or societies as associating with the *macro* or above-organismal level where focus lies on the *group*. Within evolutionary biology, groups or *populations* are classically understood as outcomes of evolution (rather than as actors). How the cultural, linguistic, and the sociological can subsequently be understood as an actual part of the evolutionary process often translates into a study of how these phenomena can be reduced to a *meso* (organismal) or a *micro* (genetic, informational) level. This is the route taken respectively by *sociobiology* (E. O. Wilson, 1975) and *behavioral ecology*. Alternatively, when languages, cultures, and societies continue to be considered as part of a *macro-level*, the very nature of evolution requires a rethink as not merely being biological in kind. Then the sociocultural is also argued to evolve, and the question becomes how the sociocultural *co-evolves* with the biological. This question is examined from within *gene-culture co-evolutionary theory* (Feldman & Cavalli-Sforza, 1976; Lumsden & E. O. Wilson, 1981; Durham, 1991). These fields are now discussed in more detail.

Original research in **sociobiology** explains the evolution of "social traits" in both humans and other organisms by researching the effect these traits have, not on the survival of the individual organism displaying the social trait, but on the spread of genes that the organism shares with others. That means that organismal fitness is broadened to include the fitness of members with shared genes (Hamilton, 1963; Hamilton, 1964a, 1964b), such as kin. An original research example whereby scholars study such **kin selection** (Maynard Smith, 1964) or "inclusive fitness" (Hamilton, 1963) is (reciprocal) altruism (Trivers, 1971) as it occurs in social insects (E. O. Wilson, 1975), symbioses (Axelrod & Hamilton, 1981), warning or alarm calls of animals and birds (Maynard Smith, 1965), or cooperation in humans (Rapoport & Chammah, 1965). Another classic example is research on the relation between "parental investment" (Trivers, 1972, p. 55) that is defined as the "cost" spent on enabling certain offspring to become reproductively successful at the "expense" of other offspring, and mate preference or "sexual selection" incurred by one of the sexes for traits that can infer handicaps on survival in the other (Zahavi, 1975; Grafen, 1990).

Social traits become understood from within the *ecology/economy of nature* where they are calculated from within **game theory** (von Neumann, 1928; von Neumann & Morgenstern, 1944), as a "logic" or "evolutionary stable strategy" (Maynard Smith & Price, 1973; Maynard Smith, 1976), that is understood as if it is a rational choice or evolutionary decision. Neither organisms nor genes are in this regard understood as rational calculators, but organismal behavior is considered a strategy maintained within populations of individuals set at “maximizing” or “optimizing” survival and reproductive success, if not of themselves, then of their offspring or of otherwise genetically similar members.

Inspired by sociobiology, and as a student of Tinbergen coming in from *ethology*, Dawkins (1976, 1979), tried to think through the consequences of such an approach by introducing a *micro-level* analysis that refocuses from the effects that organismal traits have on the spread of genes, to how traits can be explained by the **genes** that are assumed to bring them forth. Accordingly, Dawkins reduces the classic unit of biological evolution, the organism or phenotype that portrays behavioral traits, to its genotype or genes that are assumed to bring forth the phenotype. By analogy with genes, he reduced the study of cultural traits to a study of **memes** that he defined as the units of cultural transmission. Memes are hypothesized to be localized inside brain structures (which is not unlike the modularity theory shortly thereafter developed by Fodor (1983)), and they are conjectured to leap from brain to brain via imitation that occurs at a phenotypic level. Dawkins (1976, p. 192) briefly compared such a process to how viruses parasitize the cells they infect. Both genes and memes are characterized as “replicators” or as “information units” that demonstrate “copying-fidelity, fecundity, and longevity” because they outlive their “vehicles” (Table 2.3). For that reason, they are considered the true units of selection (Dawkins, 1976, p. 18; Blackmore, 1999).

Table 2.3: Universal units of selection

Replicator:	Any entity able to “create copies of itself” (Dawkins, 1976, p. 15)
Meme:	“ . . . a unit of cultural transmission or a unit of imitation” (Dawkins, 1976, p. 192); “a unit of information residing in a brain” (Dawkins, 1982, p. 109); “brain structures whose ‘phenotypic’ manifestation as behavior or artifact is the basis of their selection” (Dawkins, 1982, p. 164)
Interactor:	“An entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential” (Hull, 1980, p. 318)
Culturgen:	“That which generates culture” (Lumsden & Wilson, 1981, p. 26); “a relatively homogeneous set of artifacts, behaviors, or mentifacts (mental constructs having little or no direct correspondence with reality) that either share without exception one or more attribute states selected for their functional importance, or at least share a consistently recurrent range of such attribute states within a given polythetic set” (Lumsden & Wilson, 1981, p. 27)
Lingueme:	“The paradigm linguistic replicator;” “parallel to the gene as the basic replicator in biology, an utterance is made up of linguemes, and linguemes possess linguistic structure” (Croft, 2000, p. 28)

Source: Expanded and adapted with permission from Gontier, N., & Bradie, M. (2017). Acquiring knowledge on species-specific biorealities: The applied evolutionary epistemological approach. In R. Joyce (Ed.), *The Routledge handbook of evolution and philosophy* (pp. 136–152). London: Routledge.

Shortly thereafter, Lumsden & E. O. Wilson (1981) took matters to an *epigenetic* level by introducing the **culturgen** concept to refer to Huxley's artifacts, mentifacts, and sociofacts (that they associated with behavior). Many years later, outside of the field of biology, Croft (2000) in linguistics launched the notion of a **lingueme** to investigate how linguistic traits spread within and across populations through time. The recognition that linguemes can be transferred horizontally between different languages made this scholar compare the spread of language to *hybridization*.

A search thus began for the unit and the level whereupon and whereat selection operates, and who or what benefits from selection (Lloyd, 1988). Sociobiology and memetics originally try to reduce social and cultural behavior to a *micro-genetic* rather than a *meso-organismal* or a *macro-group level*. The schools have been heavily criticized for this, with their opponents arguing that the approach (re)introduces gene-deterministic ideas which are considered too reductionist (e.g., Sahlins, 1977; Lewontin et al., 1984; Gould, 1978, 1996). To avoid these critiques, the economic study of social behavior is now alternatively characterized as a form of *behavioral ecology* (traditionally a subbranch of *ethology*) (Borgerhoff Mulder & Schacht, 2012). The most important difference with sociobiology is that behavioral ecology tries to (re)integrate a meso-level by bringing *life history theory* into the cost-benefit equations. This point is elaborated upon during the discussion of evolutionary anthropology.

An alternative to both sociobiology and behavioral ecology is **gene-culture coevolutionary theory**. This school started off by operating at a *meso-level* where they focused on how "cultural traits" are "transmitted." The classic works of Cavalli-Sforza and Feldman (1981; Cavalli-Sforza, 1971; Feldman & Cavalli-Sforza, 1976), for example, understand culture as a "phenotypic transmission system" that is based upon "individual learning" that is irreducible to cost-benefit research, genetic, memetic, or ecological in kind. Consequently, research is centered, not on the traits or how they are genetically underpinned, but on distinguishing the different "transmission modes" whereby cultural traits spread within human populations, as the result of organismal teaching and learning. According to the authors, cultural transmission can take place from parents to offspring ("vertically"), and between organisms belonging to the same ("horizontal", from peer to peer) or to different generations ("oblique", from unrelated older to younger generations, for example, from teachers to students) (Table 2.4). More recently, Gontier (2007) and Sukhoverkov and Gontier (2021) have also pointed out the importance of "reversed transmission" (from younger to older generations) and "reticulate transmission" that occurs between members belonging to different lineages (e.g., different cultural or linguistic communities).

Gene-culture co-evolutionary theory has demonstrated how culture can actually alter the course of biological evolution. Lactose tolerance (Aoki, 1986; Feldman & Cavalli-Sforza, 1989), for example, was induced by cultural rather than biological selection. Consequently, cultural selection can be viewed as "co-evolving" with natural (genetic) selection.

An extension of gene-culture co-evolutionary theory goes by the name of *dual-inheritance theory* (DIT; Boyd & Richerson, 1985; Richerson & Boyd, 2005). While DIT

Table 2.4: Transmission in symbolic evolution

Vertical	From parents to offspring or progenitor to progeny (Cavalli-Sforza & Feldman, 1981)
Oblique	From older to younger generations (Cavalli-Sforza & Feldman, 1981)
Reversed	From younger to older generations (Gontier, 2007; Sukhoverkhov & Gontier, 2021)
Horizontal	Peer-to-peer (Cavalli-Sforza & Feldman, 1981) or between members of the same lineage
Reticulate	Between members of different lineages (Gontier, 2007, 2021; Sukhoverkhov & Gontier, 2021)

scholars recognize culture to be rooted in biology, contrary to early sociobiologists, they understand cultural evolution as irreducible to the study of genes. Instead, and herein following Campbell (1960) who was one of the founders of evolutionary epistemology, adherents of DIT theory understand selection as a universal phenomenon that extends genetic selection and that includes cultural selection (Boyd & Richerson, 1985, p. 11).

Campbell (1974) had argued that while selection was first described in biology, it pertains to more general phenomena present also in cultural and linguistic evolution. He therefore introduced a more general framework whereby scholars can think about the nature of selection, that he called the "blind-variation-and-selective-retention" **heuristic**. When a trait varies blindly and is selectively retained, such a trait can be identified to evolve by means of selection, regardless of whether that trait is genetic, social, cultural, or technological in kind. Such a heuristic thus enabled scholars to apply evolutionary theory outside of the field of biology. A couple of years later, Lewontin (1970, p. 1) introduced a "logical skeleton" of natural selection that he called "phenotypic variation," "differential fitness," and "fitness heritability." This skeleton nowadays underlies the generalized Darwinian framework whereby scholars such as Mesoudi, Whiten, and Dunbar (2006; Mesoudi, 2016) propose to study cultural evolution evolution. Table 2.5 lists additional universalized formulas of selection.

Adherents of DIT theory have also emphasized that cultural evolution can proceed differently from Darwinian selection. Social learning, for example, is recognized to be more "direct" (involving a copying of the phenotype rather than genes) and "biased" (e.g., toward specific content or it is dependent upon the frequency of transmission) than Darwinian selection is generally assumed to be (Henrich & Gil-White, 2001; Henrich & Boyd, 1998; Henrich & McElreath, 2003, pp. 129–132). Recognizing the role of the organism in the shaping of cultural evolution has moreover given way to a cultural expansion of ecological and cognitive niche construction theory (Laland et al., 1995; Odling-Smee et al., 1996).

Situating the sociocultural along the rungs of an evolutionary hierarchy thus always associates with a search for the units of sociocultural evolution as well as with identifying the locus or level where these units evolve, and identifying how they can evolve.

Table 2.5: Universal *heuristics* of selection theory

Blind variation and selective retention (Campbell, 1960)
Conjectures and refutations (Popper, 1963, 1972)
Phenotypic variation, differential fitness, fitness heritability (Lewontin, 1970)
Replication, variation, environmental interaction (Replicator, interactor, lineage) (Hull, 1980; 1981)
Blind trial and error learning (Skinner, 1986)
Generate, test, regenerate (Plotkin, 1994)
Variation, competition, inheritance (Mesoudi, 2011)

Source: Expanded and adapted with permission from Gontier, N., & Bradie, M. (2017). Acquiring knowledge on species-specific biorealities: The applied evolutionary epistemological approach. In R. Joyce (Ed.), *The Routledge handbook of evolution and philosophy* (pp. 136–152). London: Routledge.

Multi-level and group selection

As explained in the previous section, Dawkins (1976, 1982) had argued that "replicators" are the true *units* of selection, and that they need to be distinguished from the "vehicles" that house them. Examples of vehicles include chromosomes, cells, organisms, or groups, and such vehicles can be understood as *levels* of selection (Brandon, 1982). Levels of selection are traditionally understood as places or loci where genes become the *target* of selection. The idea grounds **multi-level selection** theory (Figure 2.4) that in the strict sense only recognizes genes as units of selection, but the selection of genes can occur at different levels.

These ideas, however, stand in sharp contrast to the notion of **group selection** (Wynne-Edwards, 1962, 1986) which posits *groups,* rather than genes or organisms, not as targets of selection, but as *beneficiaries* of the selection of (genetically underpinned) biological, social, or cultural traits (Lloyd, 1988). This presents another way whereby scholars understand multi-level selection.

Group selection theories were originally fiercely contested from within the field of evolutionary biology. Williams (1966), for example, assumed that traits need to be understood by the genes that bring forth such traits, not by the effects they have on groups. This was one of the reasons why Dawkins (1976) distinguished replicators from their vehicles, and why he claimed that replicators are the ultimate survivors and thus the "true" units or targets of selection.

In reply, D. S. Wilson & Sober (1994), who respectively come in from the field of evolutionary biology and philosophy of biology, suggest considering "groups as vehicles" or *levels* of selection. On their view, while social traits such as self-sacrificial or cooperative behavior can be maladaptive for the individual organism, they can be "good for" the group (D. S. Wilson & E. O. Wilson, 2006), and this can give the advantage *between*

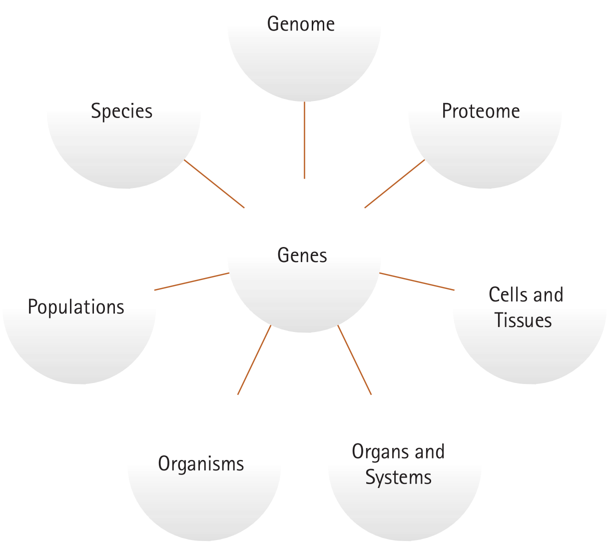

FIGURE 2.4: Schematic of multilevel *selection* theory in the strict sense. Assuming that genes are the *only* units of selection, they can be the *target* of selection at multiple levels.

Source: © Nathalie Gontier

groups. Groups whose members cooperate have an evolutionary advantage over those where the members do not.

The argument is reinforced by the assumption that groups can demonstrate "properties of functional organization" similar to that of "organisms" (Clarke, 2010; Buss, 1987; Godfrey-Smith, 2013). Here they refer to individuals that function in a group in such a way that they form a "superorganism" (D. S. Wilson & Sober, 1989). In this regard, multilevel selection theory can be understood as an attempt to bring the societal or superorganic into evolutionary study.

Group selection theory developed mainly as a means to understand "eusocial behavior" (Batra, 1968). This is "social" behavior characterized by "the division of labor" in "brood care" amongst "cooperating" members of a "group." An example is the eusocial behavior found in insect societies such as bees or ants, where sterile workers cooperate *for* the survival of their queen and her progeny. Eusocial behavior is understood as good for the group (Nowak et al., 2010) and not, as inclusive fitness theory understands it, as good for the genes shared by the group (Abbot et al., 2011). When groups demonstrate such "synergist" or cooperative organization (Corning, 1983, 2018), they are considered as marking the onset of a "major evolutionary transition" (Maynard Smith & Szathmáry, 1995). For this reason, multi-level selection theory (Okasha, 2006) relates to the rise of **hierarchy theories** (Eldredge, 1985) where taxa above populations are understood as "individuals" (Ghiselin, 1974) and as "interactors" (Hull, 1980; Sukhoverkov & Gontier 2021).

In an influential paper in the journal *Science*, D. S. Wilson and E. O. Wilson (2006, p. 327) then extrapolate and suggest that "multilevel selection theory can provide a more solid foundation for sociobiology." Simulations demonstrate that "Selfishness beats altruism within single groups. Altruistic groups beat selfish groups" (D. S. Wilson & E. O. Wilson, 2008, p. 335). In other words, *between*-group (competitive) interactions can lead to the selection of (cooperative) "other-oriented behavior" *within* a group.

INFORMATION VERSUS MEANING

As diverse as they might appear, the fields of genetics, ethology, psychology, sociobiology, gene-culture co-evolution theory, and 4E cognition all work under the premise that the entities they study are information-carrying systems. This metaphor stems from communication theory (Shannon, 1948; Shannon & Weaver, 1949) and systems theory (von Bertalanffy, 1950), and this **information** metaphor later becomes complemented by a **meaning** metaphor that arises in the field of (bio)semiotics.

Communication theory (Shannon, 1948; Shannon & Weaver, 1949) originates in association with the technological, telecommunication, and the computer sciences where scholars investigate how "messages" become "encoded" into "signals" or "signs" and how they are "transmitted" between "senders" and "receivers." This jargon underlies how scholars conceptualize information and this information metaphor then becomes systematically applied within the biological and sociocultural symbolic sciences. Genes or memes or other replicators, for example, are considered to encode for information that is transmitted over populations in time. In psychology, the brain becomes understood as a computational device that provides "output" based upon received information "input." In ethology (Lorenz, 1939; Tinbergen, 1952; Hinde, 1981) and behavioral ecology (Krebs & Dawkins, 1978; Maynard Smith & Harper, 1995; Maynard Smith, 2000), information is said to either be unintentionally "broadcasted" or intentionally "communicated" in the form of **cues** or **signals** within and between species. In sociobiology, the information transmitted is examined for its "costliness" (how with a minimum of loss and a maximum of gain, transmitted information can be "optimized" to benefit survival and reproduction), or "information value" (how it can become "trusted" and distinguished from "deceptive" information), and how the latter can be safeguarded from "freeriders" (Searcy & Nowicki, 2005). In gene-culture coevolutionary theories, scholars examine how cultural artifacts are "transmitted." In 4-E cognition theories, understanding artifacts, mentifacts, or sociofacts as extensions of cognition, or understanding an organism as embodying cognition, implies that these facts or the organism as a whole somehow "store" or carry information. With the search for a universal "heuristic" of evolution, the mechanism of natural selection becomes understood as an "algorithmic" or rule-abiding learning system.

The introduction of communication and information theory therefore induces a shift in focus from *organisms* at a meso-level to (populations of) *information-carrying entities* at a micro- and macro-level. This move is intensified by **systems theory** (von Bertalanffy, 1950), that understands an organism or "automaton" as constituted by different functional information-carrying systems that together bring forth behavioral and cognitive activity.

Systems theory evolves in association with the technological sciences that study and develop automata or machines and other "agents." Examples include self-perpetuating mechanical clocks, computers, robots, or telecommunication systems (Neumann, 1963; Turing, 1950). These non-organic "rule-following" entities demonstrate some type of "behavioral autonomy" or "agency" in how they solve problems that becomes understood as *cognitive*. As such, they exemplify how knowledge can be dissociated from self-conscious, rational, and knowing organisms at a meso-level and how knowledge can be compartmentalized and reduced to unconscious and unknowing *information units* at a micro-level. For this very reason, research on *knowledge* as the cognition and behavior portrayed by organisms has shifted to research on *information* and how it is contained and transmitted in organic and non-organic vehicles and their components.

Complex information-carrying systems later become understood as "complex adaptive systems" (Holland, 1975) that portray higher-level traits that enable the parts to function and to actually bring forth a whole that displays "emergent" properties. Research on how information "flows" within and between systems is then something that is taken up by the school of **cybernetics** (Wiener, 1948). While game theory and decision theory survey the structure or the "rules" of a system, cybernetics investigates how such rule-governed information brings forth "self-regulation," or what Maturana & Varela (1980) call *autopoeisis*. Cybernetics here meets with research on teleonomy, choice, interpretation, and *meaning* making that then starts to complement the information metaphor.

Semiotics and **biosemiotics** (Igamberdiev, 2011; Favareau, 2007; Favareau et al., 2017; Kull et al., 2011; Sebeok, 1994; Sharov & Vehkavaara, 2015; Wheeler, 2020) analyze the *meaning* or **semantics** of information. Understanding the meaning of broadcasted or transmitted information requires "interpretation," and here is where a cue or a signal turns into a **sign**. Rather than analyze information per se, and in a digital or dual sense as something that is present in objects and that is instantly understood by individuals, or as something that is sent and received, biosemiotics adds an additional layer by studying how "semiosis" or the sign-meaning process evolves, that is, how it is produced, communicated, and interpreted by the individual.

One group of biosemioticians in this regard mostly draws on the semiotic theory of Peirce (1931–1935) who understood a sign as the outcome of a tripartite relation between an "object" (in the world or in the mind), a "representamen" or "signifier" of that object (which can be an icon, index, or **symbol**), and an "interpretant" (an observer or meaning maker) who comes to an understanding of what is "signified" (Figure 2.5). In line with the tenets of **pragmatism**, these views imply that there is no interpretation-free information and no direct interaction between an organism and the world.

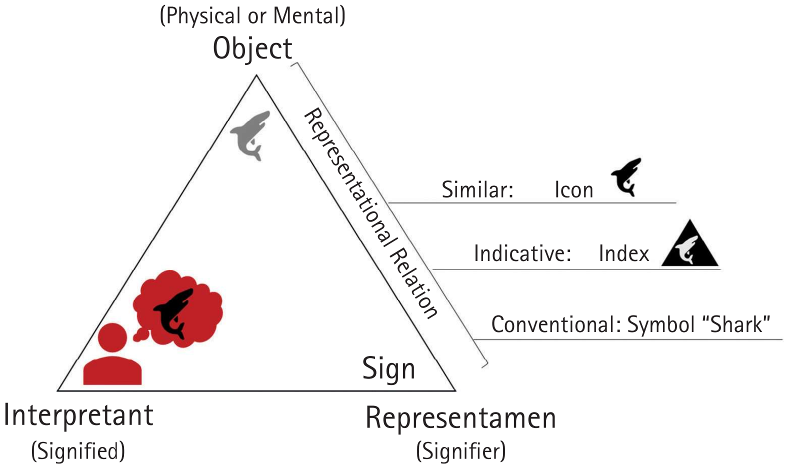

FIGURE 2.5: Signs as a relation between object, representamen, and interpretant according to Charles Sanders Peirce. While Peirce still endorses a representational relation between object and sign, he already emphasizes the role of the interpretant in meaning construction.

Source: © Nathalie Gontier

On the contrary, sign formation and interpretation always already involve a cognitive construction process. A second group of bio-semioticians therefore includes research on how signs underlie the construction of a cognitive and ecological niche or "Umwelt" (von Uexküll, 1921, 2001). Different organisms belonging to a variety of species interpret the world differently, and they evolve different ways of being in the world. This *Umwelt* concept later served as a direct inspiration for Lewontin's (2000) "niche construction" concept where organisms are understood to reform and construct their world.

A third group active in the field of biosemiotics, however, tries to reduce the study of the meaning-making process that the first two groups situate in interpretative signs and niches, to a micro-level, by searching for "informational codes" (Barbieri, 2014). This, for many in the field, is considered a setback, because such a study again implies a reduction of semantics to information.

Today, the information metaphor is more and more becoming complemented by the meaning metaphor and we can also diversify disciplines based upon which metaphor they implement into their research. Gene-culture co-evolutionary approaches, for example, continue to explore how biological and cultural objects are "transmitted" (Richerson & Boyd, 2005). Interpretative approaches (Geertz, 1973) instead consider how cultural ideas are "transformed" and how meaning and understanding at a cultural level results from interaction, interpretation, and representation (Sperber, 2000; Claidière Scott-Phillips & Sperber, 2014). This helps to understand why *pragmatism* links to *enactment theory* that substantiates **symbolic interactionalism** (Mead, 1938), and why 4-E cognitive views relate to *connectionist* and *general purpose approaches* to cognition (Elman et al., 1996), as well as to the study of the **ecology of mind** (Bateson, 1972) or culture (Rappaport, 1979).

EXPANSION OF THE SYMBOLIC EVOLUTION SCIENCES

New symbolic sciences have evolved from these diverse backgrounds, including evolutionary psychology, evolutionary linguistics, evolutionary anthropology, evolutionary archaeology, evolutionary economics, and evolutionary sociology. This section surveys how these symbolic evolution sciences differentially integrate the tenets of the distinct evolution schools, and how they have in so doing (r)evolutionized their classic counterparts.

Evolutionary Psychology

Evolutionary psychology is a direct outgrowth of applying the principles of social Darwinism and sociobiology to the problems of cognitive psychology (Barkow et al., 1992; Barrett et al., 2002; Goetz et al., 2009). Identifying itself as the "second wave of the cognitive revolution" (Cosmides & Tooby, 2013, p. 201), evolutionary psychology understands cognition to be inborn or innate, and therefore genetically and neurologically underpinned. Likewise, it assumes that cognitive traits evolved in the same manner as zoologists and ethologists consider that anatomical and behavioral traits evolve, i.e., by means of natural and sexual selection.

The emphasis on cognitive innateness (Pinker, 2002) makes evolutionary psychologists revolt against older cognitive psychological (Piaget, 1970) and evolutionary epistemological schools that explore the inductive acquisition of knowledge (Popper, 1963; Campbell, 1974). They furthermore object to *behaviorist* and *instructionist* schools within psychology (Skinner, 1938, 1981) that examine the role played in such knowledge acquisition by learning and instruction through, for example, operant and classic conditioning.

Yet it was within this behaviorist and constructionist context that early comparative psychological research was conducted on communication in non-human primates where gorillas, chimpanzees, and bonobos were taught to speak, sign, or communicate with pictorial languages such as Yerkish (von Glaserfeld, 1974; Lynn, this volume). Contrary to behaviorist and comparative psychologists who assume the existence of evolutionary continuity between humans and other primates, evolutionary psychologists work under the assumption that after the split with non-human primates, and during the development of the *Homo* lineage that commenced some 2.5 million years ago, human hunter-gatherers diverged from non-human and other hominin lineages by "gradually adapting" to a Pleistocene environment where they evolved unique and "domain-specific" cognitive and behavioral "adaptations." To understand current human behavior, scholars manifest that research needs to be done on the nature of this "environment of evolutionary adaptiveness." In practice, that often means that researchers are on the lookout for the *ultimate* causes or the survival value and reproductive benefit of (unique) human behaviors such as parental care and infanticide, sexual conflict and romantic love, cooperation, and competition.

These cognitive and behavioral adaptations are assumed to take on the form of domain-specific modules in the mind, and evolutionary psychologists thus try to place Fodor's modularity theory into an evolutionary context (Sperber, 2001). Hypothesized modules are characterized as "evolved computational systems, engineered by natural selection to use information to adaptively regulate physiology and behavior" (Cosmides & Tooby, 2013, p. 201). Some of these hypothesized adaptations, being tailored to an older environment, can today decrease fitness, and here evolutionary psychologists oppose themselves to the rational choice and game theoretical approaches endorsed by the schools of *sociobiology* and *behavioral ecology*. Instead, in their search for modules, evolutionary psychologists connect to genetic and brain imaging research, and this relates to research on the *proximate causes* of behavior.

Natural selection theory is internalized and applied to the study of the brain that consequently becomes demystified from the "black box" (Turing, 1950) it was once thought to be. Cognition is understood as an outcome of evolution, like any other organismal feature is. Specific cognitive or behavioral genes or cognitive modules that the school assumed to exist, however, are rarely identified, and many scholars outside the field of evolutionary psychology instead continue to prefer a "domain general" and gene-free approach to cognitive research (for discussions, see Whitehouse, 2001).

Conjointly, scholars active in *evolutionary epistemology*, *eco-evo-devo*, and *4E cognitive approaches* have long opposed both computational and modular approaches to cognition. Instead they understand cognition as the outcome of a tripartide relation between brain-organism-environment. Evolutionary psychology's emphasis on *passive* selection and adaption to an ancestral environment is therefore considered a setback or impediment for recognizing the important role played by *learning,* as well as *construction,* in the evolution of symbolism at a cognitive, cultural, and ecological level. These latter views tone down Panglossian adaptationist views, and they make way for the recognition that traits are often "co-opted" or "exapted" over the course of evolution (Gould & Lewontin, 1979; Gould & Vrba, 1982; Lickliter & Honeycutt, 2003; Bolhuis et al., 2011). Contrary to evolutionary psychologists, these latter schools include data coming in from *eco-evo-devo* and *reticulate evolution* schools, that beyond natural and sexual selection, identify numerous supplementary mechanisms and processes that can influence human symbolic evolution, and these neither need to occur gradually nor exclusively in the past. The microbiome, for example, as well the sociocultural environment, impact the evolution and development of cognition. The human species is constantly and continuously evolving, sometimes at a fast pace, and there is thus no reason to believe that our minds or bodies are stuck in our evolutionary past.

Evolutionary Linguistics

The cognitive turn that opposes the behavioral one, together with the turn toward innateness and biological research on cognition that opposes research on learning and the role played by culture, is actually inspired by research in **traditional linguistics**. This is because cognitive thought has long been understood to be linguistic in kind. That is the reason why scholars have searched for a "language of thought" (Fodor, 1975), or for some other type of central processor that is understood as "computational," "rule-governed," and therefore "hierarchical" or "compositional" (Chomsky, 1982).

Such ideas go back to the works of Chomsky (1959) who, against Skinner's (1957) ideas put forward in the latter's *Verbal behavior* volume, raised what later became known as the "poverty of stimulus argument;" the idea that language cannot develop from learning alone because children are often exposed to imperfect examples. In line with Lenneberg's (1967) research on the existence of a "critical period" for language learning, Chomsky (1982) proclaims that the "faculty" of language is an innate "organ" in the brain.

Chomskyan linguistics inspects the "synchronic" aspects of the hypothesized language organ, which means that from within functional-structuralism, language becomes understood as an ahistoric, functional or self-contained, complex system. Focus lies on the structure of language, and that translates into research on syntax (Chomsky, 1957, 1965). Through its adherence to synchronic research, Chomsky opposes "diachronic" or *historical linguistics* as well as *anthropological linguistics* that respectively analyze the historical *diffusion* of tongues and the role played by culture in this societal phenomenon.

Chomsky furthermore proclaims that *communication studies* conducted by ethologists, comparative psychologists, and primatologists (Lynn, this volume; Leavens & Bard, this volume), neither in humans nor in human-ape comparisons, lends insight into the nature of human language. That language enables communication for Chomsky is secondary to the cognitive tool that language is for enabling "creative thought processes." The latter, he asserts, is lacking in our evolutionary relatives, and he claims the discontinuity of language rather than continuity from ape communication systems.

Language as an "innate acquisition device," or as a "computational bioprogram" subsequently becomes investigated by *biolinguistics* (Anderson & Lightfoot, 2000; Bickerton, 1984; Jenkins, 2000) that starts to associate with those branches of psycholinguistics and neurolinguistics that steadily map the different brain regions involved in language (Boeckx & Piattelli-Palmarini, 2005; Stowe & Haverkort, 2005). These schools can be understood as forerunners of *evo-devo* research because they try to elucidate language *evolution* by examining language structure and language *development* in humans so as to acquire insight into the nature of a hypothesized "protolanguage" Ruhlen, 1994).

Regarding this structural study, much work on protolanguage has been done by internal reconstruction methods. In addition, data on the development of child language, younger languages such as Pidgins and Creoles, and language pathologies, have often been taken as a base point from which to hypothesize the nature of protolanguage (e.g., Bickerton, 1984). In their research, scholars mainly remain language-oriented, because in their attempts to explain their subject areas from within an evolutionary biological perspective, they often reach the limit of the explanatory scope provided by natural selection theory. They have therefore sought solace in critiques of the Neo-Darwinian synthesis, and in non-adaptationist and systems theoretical or constructivist views on both cognition and evolution (Gould & Lewontin, 1979).

Both traditions are then countered by Pinker and Bloom (1990), who come in from within the field of evolutionary psychology. Heavily inspired by Dawkins, in an influential paper in the journal *Behavioral and Brain Sciences*, they state that language shows "design" and that it is an "adaptation" that must have evolved gradually by means of natural selection *for* "the communication of propositional structures." This paper is nowadays often taken as foundational for the field of **evolutionary linguistics**. A reply eventually comes from Hauser et al. (2002) in *Science*, wherein they distinguish between the "faculty of language in the broad sense" (FLB) and the "faculty of language in the narrow sense" (FLN) (Table 2.6).

The FLN contains the hypothesized cognitive capacity for "MERGE" that enables "recursion" required for compositional thought, and the former contains the "sensori-motor" and "conceptual-intentional system." Only FLN is argued to be uniquely human, while aspects of FLB are now recognized to be present differentially in different organisms. In this paper, they furthermore repeat their position that homologous structures must have been rapidly "exapted" or "co-opted" (Gould & Vrba, 1982) from other contexts (such as tool use or social intelligence) for human language (Hauser et al., 2002, p. 1572). Polemic debates then follow in several 2005 issues of the journal *Cognition*.

Evolutionary linguistics is additionally intricately connected with *computational linguistics* that has quickly hopped on board the adaptationist train coming in from evolutionary psychology, by helping to simulate the "design features" of language (Hockett, 1960). Such is possible because as a tradition that surpasses evolutionary psychology in time, computational linguistics already leaned closer to *information* and *communication* theory. Language, both natural and artificial, is understood from *system theoretical* and *cybernetic* jargon as a "complex adaptive system" (CAS; Holland, 1975) that works

Table 2.6: The faculty of language in the broad and narrow sense according to Hauser, Chomsky, and Fitch (2002)

Faculty of language in: the narrow sense	P0 the broad sense
Recursion	*Sensori-motor system* (vocal imitation and invention, neurophysiology of action perception schemes, discrimination of sound patterns, biomechanisms of sound production, and modalities of language production and perception)
	Conceptual-intentional system (theory of mind, the ability to acquire non-linguistic conceptual representations, referential vocal signals, imitation, and voluntary control of signal production).

according to algorithmic rules and heuristics whereby it is able to self-regulate and optimize over time. Such CAS approaches are directly inspired by Darwinian population genetics and they form a uniform language for cybernetic *control theory*, *game theory*, and *complexity theory*.

The origin and evolution of language features thus becomes the subject of computational models that simulate how single and multiple agents evolve conventional agreements on aspects of language (de Boer, 2006; Steels, 2002, 2011). The notion of *linguistic replicators* and how they spread over populations in time plays a significant role in these debates (Szathmáry, 2000). These *micro-level simulations* of how replicators spread amongst populations subsequently become complemented with *meso-level experiments* on how artificial agents, robots, and humans, *transmit* and *construct* aspects of language such as a lexicon or syntax at a *cultural* level, through "iterated learning" (Smith et al., 2003; Tamariz, 2014).

By integrating psychological work, emphasis has also come to lie on how learning stems from "shared intentionality" (Leavens & Bard, this volume; Racine et al., 2014; Tomasello, 1999) and how this brings forth shared *meaning*. This brings forth *constructivist* and *biosemiotic* perspectives (Donald, 1991; Zlatev, 2014), where evolutionary linguists meet again with ethological and comparative, behavioral, and cognitive scientists in order to compare how communication, intersubjectivity, and meaning-making occurs in our closest living primate relatives or in other organisms (Okanoya, 2012).

Finally, under the influence of big data mining, and by borrowing new tools developed in biological phylogenetics, *macroevolutionary research* is reentering the fields of anthropological and historical linguistics, where scholars model the evolution of language families (Atkinson et al., 2008; Carling et al., this volume; Gray et al., 2009; Levinson & Gray, 2012). Beyond the classic *vertical* tree models, linguistic phylogenetics are now able to commence a mapping of the massive occurrence of *horizontal* transfer that occurs in language evolution, through language contact, word borrowing, linguistic blending, etc. (List et al., 2016), and this requires the introduction of reticulate evolution jargon.

Evolutionary Anthropology

Traditional anthropology is a diverse field that includes subdisciplines such as physical and paleoanthropology that study hominin fossil remains; archaeology that studies the cultural remains of hominins; biological anthropology that analyzes current human anatomy and physiology; medical anthropology that inquires into human health and disease; cultural anthropology that analyzes cultural groups; social anthropology that examines social groups and systems; and linguistic anthropology that investigates human languages. None of these fields deny the evolutionary origin of our species, but not all are centered on studying humans from within that evolutionary context. Physical, medical, and biological anthropology, for example, lean closer to medical and forensic research, and the other fields lean toward their respective classic counterparts that include art history and archaeology, folklore and (multi)cultural studies, sociology, and linguistics.

In so far as human behavior and cognition is indeed studied from within an evolutionary approach, anthropologists often object to both the tenets of sociobiology and evolutionary psychology, and they instead identify either with the ethological branch focused on human behavioral ecology (Borgerhoff Mulder & Schacht, 2012), or with cognitive anthropology (Bloch, 1998; D'Andrade, 1995; Strauss & Quinn, 1997; Beller et al., 2020) which connects to phenomenological schools within *cognitive psychology*.

Ecological approaches in anthropology scrutinize culture(s) in relation to their environmental settings. Original approaches reach far back in time and first become formulated in adaptationist jargon, in terms of "subsistence analyses" by Morgan (1877) and "energetics" by White (1943). Later they are formulated in the form of variants of "Umwelt" or "niche construction" theories by Steward (1955), Frake (1962), Vayda (1969), Rappaport (1968, 1979), and Bateson (1972). Interesting here is that with this transition from adaptationist to constructionist views, the schools involved undergo transitions in their epistemic outlook, from "universal" and "unilineal" views to "historically-particular" or "multilineal" views on human cultural evolution.

Unilineal views are formulated early on in evolutionary cultural research. Morgan (1877), for example, introduced a stadial, social progressivist theory of human society that he understood as running through "lower", "middle", and "upper" "stages" of "savagery" and "barbarism," to "civilization." He suggested that these stages are universal and accompanied by different "arts of subsistence." These include "foraging or gathering" fruits and roots in natural environments; "fishing" and expanding into aqueous environments; "farinaceous subsistence" and cultivating cereals and plants such as spelt, rice, oats, or rye; "farming" and domesticating animals that provide a constant source of meat and milk; and "agriculture" that involves significantly altering the environment. These subsistence strategies served to mark distinct stages of "social development," and he linked these to different societal structures and family and kinship systems.

Inspired by Morgan, White (1943, p. 338), attempted to calculate how culture evolves globally by measuring the amount of energy gained from labor and rising technologies that for him include animal husbandry, agriculture, and the use of fossil fuels. His "law of cultural evolution" stated that "culture develops when the amount of energy harnessed by man per capita per year is increased; or as the efficiency of the technological means of putting his energy to work is increased; or, as both factors are simultaneously increased."

Both Morgan and White's theories are *unilineal* because they assume a *universality* and *directionality* to cultural change. Still formulated in *social progressivist* jargon typical of the nineteenth century, these theories are sometimes classified as *neo-evolutionist*, and they are the cultural equivalent of *orthogenetic* theories in biology. Today, these theories are discredited and recognized as scientifically and often also politically incorrect.

Early in the twentieth century, the older unilineal views become countered by *multilineal* views (Steward, 1955) that link *ecological* approaches to *phenomenological branches of cognitive psychology*. Rappaport (1968, 1979), for example, brought cognition into the equation by distinguishing the physical human–environment interface that he called an "operational environment" from the "cognized environment" that refers to the particular cognitive ecology engendered by the former. In this regard, multilineal ecological anthropology serves as a means to bring into evolutionary context older research on *pragmatism*, *cultural relativism*, and *historical particularism* that investigate and recognize human cultural diversity and particularism or uniqueness. It is these schools that introduce niche construction perspectives through investigating the creation of an ecological *Umwelt* (von Uexküll, 1921, 2001) and cognitive *lifeworld* (Husserl, 1936) that underlies culture-specific *worldviews* (James, 1909).

Ecological anthropology directly links to *cybernetics* and *biosemiotics* on the one hand, and on the other, early *evo-devo* and *constructivist* schools that underlie *dialectical* views on how organisms relate to the environment. These bring forth *4E cognition* research that founds cognitive anthropology (D'Aquili et al., 1979; Rubinstein et al., 1984).

A new wave of *ecological* evolutionary research then emerges in the late 1970s that, inspired by sociobiology, examines the relation between cultural anthropology and Darwinian evolution theory, and this school now goes under the name of **evolutionary anthropology** (Chagnon & Irons, 1979; Irons & Cronk, 2000). Research within this school has shifted from the *micro*, genetic to the *organismal meso-level*, and from the study of *proximate* to *ultimate* causation. Following Grafen (1984, pp. 63–64), this shift from the genotype to the phenotype occurs under the adherence to the "phenotypic gambit" that:

> … examines the evolutionary basis of a character as if the very simplest genetic system controlled it: as if there were a haploid locus at which each distinct strategy was represented by a distinct allele, as if the payoff rule gave the number of offspring for each allele, and as if enough mutation occurred to allow each strategy the chance to invade.

In other words, even without knowing the particulars of how genetics and inheritance underlies behavior, it is assumed that selection favors those traits that increase fitness.

A large group of evolutionary anthropologists thus tries to distinguish itself from older *social Darwinism* and *sociobiology* by leaning closer to *behavioral ecology*. Nonetheless, these varied fields all study similar phenomena. This results in each field introducing different terminology to refer to similar research topics. Examples of such converging topics include research on "kinship systems" and the role of "altruism" or the "(extended) family" in "child rearing" (kin selection and parental investment), and "sexual behavior" (sexual selection) (Betzig et al., 1988; Nettle et al., 2013; Winterhalder & Smith, 2000). Another example is "optimal foraging theory" which continues exploring the relation between diet, energy consumption, life style, and societal system (Pulliam, 1974; Stephens & Krebs, 1986; Smith et al., 1983; Hill & Kaplan, 1992). Theoretical outcomes of such research include the "expensive tissue hypothesis" that links big brains to a reduction of the gut in turn brought forth by an increase in meat consumption (Aiello & Wheeler, 1995); or the "vocal grooming hypothesis" (Dunbar, 1995) that correlates neocortex size to group size and that is considered to play a role in the transition from manual to spoken language.

Operating on a *meso-level*, human behavioral ecology nowadays also takes *life history research* into account. Originally, such research was formulated in strict adaptationist terms, and the focus lay on calculating the energetics and tradeoffs of certain traits. But today the field leans closer to *evo-devo* research because it examines "life cycles," "evolutionary constraints," and "phenotypic plasticity" (Fabian & Flatt, 2012; Flatt & Heyland, 2011; Hill & Kaplan, 1999; Nettle & Frankenhuis, 2019; Stearns, 1992).

On a *macro-scale*, cultural phylogenetics is cross-fertilizing with biological phylogenetics to model aspects of cultural evolution on the grand scale (Jordan & Huber, 2013; Tehrani & Collard, 2002; Bentley & Shennan, 2003). Much current work is set on applying evolutionary anthropology to contemporary macroscale issues of global warming and climate change or urbanization (Gibson & Lawson, 2015; Caudell & Quinlan, 2016). Finally, it is also within this tradition that Turchin's (2003) "cliodynamics" can be situated. Cliodynamics applies population genetics and cultural phylogenetics to understanding the societal overturns that characterize social history. The research is set to find how individual and within- and between-group dynamics underlie the rise and fall of empires, and it links to the idea of "multi-level cultural selection" because it has demonstrated that within-group cooperation is advantageous in between-group competition.

Evolutionary Archaeology

Traditional archaeology classically studies the material remains of past cultures (art works, tools, or ruins of lost civilizations). As the number of ancient archaeological sites and hominin fossil finds increased, a first group of **evolutionary archaeologists** has co-evolved with paleoanthropologists (Tattersall, this volume), and paleoanthropology has mostly taken a *meso*, and *macroevolutionary* research outlook because of their interest in the evolution of different hominin species.

Hominin species are defined and distinguished based upon organismal traits, mostly skeletal and dental features. By tracking these organismal features over deep time across species, scholars then look for *macroevolutionary trends*. Examples of the latter are the general reduction across hominin species in skeletal robustness or teeth size, and the increase in brain size.

A considerable amount of research in paleoanthropology and archaeology is also spent on dating the fossils and material remains, and in correlation, on measuring the pace whereby hominin and cultural evolution occur. Here, the fields have been divided between *lumpers* and *splitters*. The former and older school long assumed a *gradual* and (uni)linear evolution from *Homo habilis* to *Homo erectus* to *Homo sapiens,* with different fossil finds and material remains being considered as variations stemming from the same species. By contrast, the latter, younger school recognizes the different fossil and material cultural finds as stemming from different species. Hominin evolution is subsequently characterized as following either a *gradual* evolution pattern or a pattern of *punctuated equilibria* (Tattersall, this volume; Eldredge 1985).

The debates have furthermore associated with older multilineal or *multiregional* (Wolpoff et al., 1988) versus unilineal, *out of Africa* (Stringer & Andrews, 1988) scenarios. But today, as a result from data obtained from modern and ancient genetic studies, these models are being replaced by studies on the *multiple migration waves* that came out of Africa, and how distinct populations and species merged through *hybridization* or *backcrossing* (Kelso & Prüfer, 2014).

On a *meso*-level, evolutionary archaeologists investigate how material remains provide insights into the origin of organismal behaviors such as hunting and gathering, the mastery of fire, cooking, the production of tools, clothing, and dwelling skills. By analogy with the anatomical distinction made by paleoanthropologists between "archaic" (more robust) versus "modern" humans, archaeologists have in this context debated which behavioral traits are "archaic" versus "behaviorally modern" (Majkick, this volume; Nowell & Cooke, this volume; Power et al., this volume). This debate has centered mostly on the status of Neanderthals (Zilhão, 2001; Mithen, 2005), but also other hominins have been examined for how behaviorally modern they were. In comparison to humans, Neanderthals, Denisovans, *Homo floresiensis* (Brown et al., 2004), and other anatomically archaic specimens, have now been demonstrated to portray behavioral traits that are traditionally classified as *modern* and typically human. Examples of such traits are the use of pigment and the exploitation of marine or avian resources.

These findings counter older ideas that symbolic behavior appears rapidly, during the European Upper Paleolithic (Klein, 2000; Mellars & Stringer, 1989) and that symbolic behavior is portrayed exclusively by modern humans. Instead, modern symbolic behavior is now often situated as arising in the Middle Stone Age (Stringer & Mellars, 2007). Findings that substantiate this claim are perforated shell beads indicative of symbolic behavior, and geometric engravings found on pigment extracted from the South African Blombos cave (Henshilwood & Marean, 2003; Vanhaeren et al., 2006). As to the pace whereby symbolic behavior emerges, McBreaty and Brooks (2000) are famous for endorsing a *gradual* scenario, while especially d'Errico (2003) has maintained a *punctuated equilibria* and historical particular view, arguing that modern behavior has evolved multiple times over, in distinct hominin species.

The *archaic* versus *behavioral* modernity debate has also been expanded toward research on the origin of modern cognitive, symbolic behavior (Donald, 1991; Malafouris & Renfew, 2010; Iliopoulos & Malafouris, this volume). Herein fortified by *4E cognition theories*, scholars survey how the material and behavioral traits embody, embed, extend, and enact cognition. Such research thus includes the *ecology* or *niche* that is constructed within and around material and fossil finds. This brings forth an experimental component where scholars try and remake or actually relive the past (Toth & Schick, 1993; Kempe et al., 2012; Till, this volume). A significant amount of research in 4E archaeological traditions centers on how tools demonstrate the evolution of "compositionality" required for language (Uomini & Ruck, this volume).

At the same time, the study of material remains has resulted in an investigation into how these define the *units* of cultural change (O'Brien & Lyman, 2002; Shennan, 2002), and how cultural change can be modeled in Darwinian terms (Mesoudi, 2017), or in cultural *phylogenetics* (Mendoza Straffon, 2016; O'Brien & Lyman, 2003). Cultural artifacts have also become modeled in evolutionary tree and network diagrams that depict how these traits, like genes, memes, or linguemes, evolve.

Finally, the debate on the need to extend the evolutionary synthesis is now entering evolutionary archaeology (Prentiss, 2021), through, for example, debates on the importance of niche construction in relation to the rise of agriculture and the domestication of animals (Zeder, 2018).

Evolutionary Economics

The field of **traditional economics** precedes evolutionary theory through theorizing on the nature and division of labor (Mandeville, 1714), and the wealth of nations (Smith, 1776). Economy has from the onset been conceptualized as a relation between the "individual" and the "state" or the "institution." Research has focused on how the individual has "needs" resulting from subsistence that are or are not met by the state due to how it handles the "distribution of natural resources" and "common goods" arising from labor, trade, commerce, or warfare. Individual needs are cast against value systems that bring in moral and political institutions that regulate economy. These institutions are considered as above-organismal structures that constrain the individual.

Later, Darwin would ask whether beyond moral and political systems, there exist natural regulators to resource access and management. Inspired by Malthus (1798) who predicted that natural population growth would lead to a "scarcity of resources," Darwin reasoned that organisms find themselves in a "struggle for existence," and this was the basis for his theory of evolution by means of natural selection. Haeckel (1866, II, p. 286) would subsequently establish the field of ecology (or "oecologie") that studies the "conditions of existence" in relation to the *biotic* and *abiotic* environment, or how organisms take their place in the "household" or "economy" of nature. How organisms interact with one another, and with the physical environment is what for Haeckel enables Darwinian adaptation (Egerton, 2013; Corning, 2010).

Ecological research ranges from micro to meso to macro scales, and also traditional economics distinguishes between micro-, meso-, and macroeconomics. These fields respectively refer to individuals and the family; communities such as social organizations or political parties; and the state, nations, or other supra- and super-organismal structures.

The term **evolutionary economics** was coined by Veblen (1898) who was a student of Charles Sanders Peirce, the founder of *semiotics*, and a colleague of the *pragmatists* John Dewey and William James. Veblen launched the concept of "cumulative causation," while Marx (1867) looked into the "dialectics" (or what is now called up and downward causation; Hodgson, 2002) that exist between the micro-, meso-, and macro-level as studied from within *evolutionary hierarchies* (Simon, 1962). From here, it's only a small step to interrogate the nature of "agency" and "control" as it would be debated in systems theory and cybernetics (Anderson et al., 1988; Arthur et al., 1997), and decision and rational choice theory (Simon, 1959; Einhorn & Hogarth, 1981; Friedman, 1998). These fields have indeed been dominating evolutionary economics.

Evolutionary economics today works from within a generalized Darwinian approach, one that it recognizes as incomplete (Hodgson & Knudsen, 2006), for it encounters similar problems faced by the other disciplines, on what the units and levels of selection are (Nelson & Winter, 1985; Gintis & Bowles, 2011; Dopfer et al., 2018). Is it organisms, their needs, or their institutions? And where do these needs find their ground? In psychological ideals, biological determinants, or sociopolitical constructs? Here too, multilevel selection (Okasha, 2006; Sober & Wilson, 1999), synergistic (Corning, 2018), extended evolutionary (Laland et al., 2015), and third way approaches (Gontier, this volume) are needed to tackle the questions.

Evolutionary Sociology

Traditional sociology is concerned with the way human individuals organize into groups, ranging from the core and extended family and villages and larger communities, to societies that are structured around power institutions such as the state or religious institutions. Following earlier structuralist, structural-functionalist, and synchronic approaches as they were introduced by scholars such as Emile Durkheim (1895), Herbert Mead (1934), and Talcott Parsons (1975), the field originally built upon the ideas of *systems theory* and it investigated how individuals *hierarchically* organize into "complex" and "functional systems" (Adams, 1988; Burns & Flam, 1987; Vayda & Rappaport, 1968) or "superorganisms" (Spencer, 1876).

Later, these systems came to be understood as "complex adaptive systems," and this shift opened the door to statistical and probabilistic analyses in general, and *game theory* in particular that founded **evolutionary sociology** (Dietz et al., 1990). Here is also where *sociobiological* research enters the scene, and where scholars search for the biological and genetic basis of altruism and cooperation; pair bonding and the rise of the family; parental care and the division of labor; incest taboos; etc. (Machalek & Martin, 2015, Lopreato & Crippen, 1999; Van den Berghe, 1975; Van Parijs, 1981). In fact sociobiology was defined by E. O. Wilson (1975, p. 4) as "the systematic study of the biological basis of all forms of social behavior, in all kinds of organisms, including man." In so far as the field finds additional inspiration in behavioral ecology, evolutionary psychology, and gene-culture co-evolutionary theory, it also probes the phenotype from within the organism-group dynamic (Blute, 2010; Barkow, 2006; Booth, 1976; Richerson, 1977). Nonetheless, traditional sociology has been quite reluctant in adopting an evolutionary approach, and today, the field is somewhat divided between evolutionary sociologists that inspect the ultimate causes of individual social behavior and social group organization (Turner & Machalek, 2018), biosociology that scrutinizes the proximate causes of social behavior (Rosa, 1979; Hopcroft, 2016; Mazur, 2004), and environmental sociology (McLaughlin, 2012) that introduces an ecological account. Sociology too is thus divided by micro-, meso-, and macro-oriented research outlooks, and debates consequently are centered on the units and levels of selection and the nature of evolutionary hierarchies or the existence of group and multilevel selection.

Beyond Theory

The new symbolic evolution sciences are an outgrowth of implementing especially Neo-Darwinian thinking into the traditional fields of psychology, linguistics, anthropology, archaeology, economics, and sociology. By doing so, these fields have often opposed older systems theoretical and more constructivist-oriented approaches. The latter approaches, however, were never non-evolutionary. Instead, they have associated more with early evo-devo and ecological schools of thought, which now lie at the basis of the newly emerging *eco-evo-devo* paradigm. In so far as the new symbolic sciences have been endorsing strict selectionist and adaptationist views, they have been evolving in opposition to these approaches.

Today, with the rise of the extended evolutionary synthesis, and the recognition of a third way for evolution, scholars are steadily breaking through these disciplinary divisions and they are starting to reconcile some of the long held grudges. The recognition of the importance of eco-evo-devo and also of reticulate mechanisms and processes of evolution is by and large the result of data-driven science rather than theory formation.

Today, theoretical approaches are trading place with empirical approaches that follow a trend toward empirical testing of some long upheld ideas. Old field work studies are complemented with micro-simulations, meso-experiments, and macro-modeling (Table 2.7).

Micro-simulations involve mathematical, game theoretical, and computational simulations that mimic how replicators such as memes or linguemes spread amongst

Table 2.7: Data-driven research

Micro-level	Meso-level	Macro-level
Replicators E.g., genes, memes, linguemes	Interactors E.g., agents, organisms, robots, machines	Communities E.g., languages, cultures, societies, populations, species
Game theoretical and computational simulations	Field work, (multi-)agent-based computational modeling, (iterated) learning experiments (including transmission chain studies), and reaction experiments	Ontological hierarchy theories, phylogenetics, and graph theories (tree and network models)

populations of (multi-) agents (Croft, 2000; Gintis, 2009; Steels, 2002; Maynard Smith & Harper, 1995; Szathmáry, 2000). *Meso-experiments* refer to (observational or iterated) learning and reaction experiments that are performed with living organisms (McElreath & Henrich, 2007; Henrich et al., 2004; Mesoudi, 2016; Navarro et al., 2018; Prinz, 2008; Richerson & Christiansen, 2013). *Macro-modeling* refers on the one hand to hierarchy theories, and on the other hand to the numerous phylogenetic and graph (tree and network) methodologies whereby scholars examine how species, populations, cultures, languages, and societies evolve (Gray & Watts, 2017; Knappett, 2013; Mace & Holden, 2005; Mace & Jordan, 2011; Shennan, 1997). These techniques and tools are now simultaneously functioning as new bridges and barriers for interdisciplinary research.

FUTURE PROSPECTS

This chapter has sketched the epistemological structure of the symbolic evolution sciences from within the perspectives of philosophy and anthropology of science. Not aiming at completeness, the above analysis provides an overview of where to find the roots of the varied disciplines, and which major controversies underlie divergence.

It is clear that the study of human symbolic evolution requires an inter- and transdisciplinary stance. Many disciplines have provided valuable data and insights into how aspects of human symbolic evolution can be understood and studied. None of these disciplines, however, have so far been able to explain all aspects of human symbolic evolution.

What is more, proof for one idea or theory does not immediately imply the falsification for another. Demonstrating that certain genes are the target of positive selection does not exclude the important role played by epigenetic and evo-devo mechanisms that underlie molecular and organismal learning. Demonstrating that individuals invent new behavioral traits does not exclude the fact that cultural rites and rituals evolve at a community level. Modeling the spread of memes or replicators does not falsify that signs require interpretation. It follows that there is not one single theory of human symbolic evolution.

Recognizing the scientific validity of epistemic pluralism brings forth new research questions that need further analysis. From an applied evolutionary epistemological point of view (Gontier, 2017, 2018a, 2018b, 2021), important issues in this regard concern the nature of **plurality**, **interaction**, **hierarchy**, and **causality**. These problems are deeply intertwined.

The triumph of the evolutionary sciences has brought to light that besides by means of natural selection, numerous mechanisms and processes exist whereby evolution occurs. These operate on multiple units ranging from replicators (Dawkins, 1976), reproducers (Griesemer, 2000), and interactors (Hull, 1981), to symbionts (Margulis, 1999) and community traits (Sukhovrkov & Gontier, 2021). These units in turn evolve at

Table 2.8: The plurality of units, levels, mechanisms, and processes of evolution

Units	Levels	Mechanisms and Processes
• Replicator (gene, meme, lingueme) • Reproducer (systems and organs, individual behaviors) • Interactor (vehicle, phenotype, agent, . . .) • Symbiont • Community traits (group ideas and behaviors, languages, cultures, artifacts, and technological complexes) • . . .	• Genome • Organism • Community (groups, species, holobionts) • . . .	• Natural selection • Sexual selection • Drift • Epigenetics • Eco-evo-devo processes • Social processes • Cultural processes • Reticulate processes • . . .

multiple levels of distinct evolutionary hierarchies (Table 2.8). Examples of such levels are genomes and organisms, as well as **communities**, and these, as entities that occupy space and time, embed the constructed social, cultural, or linguistic niches (Sukhovrkov & Gontier, 2021).

Scholars now need to come to terms with how distinct units, levels, mechanisms, and processes interact simultaneously within phenomena as diverse as the evolution of anatomical form, language, or sociocultural and economic evolution. This will enable a more comprehensive understanding of human symbolic evolution.

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