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Selectionism

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The goals of this chapter are threefold: (a) to characterize selectionism as a general approach to understanding complex phenomena as products of relatively simple processes acting over time, (b) to identify conceptual impediments to the acceptance of selection by reinforcement as the central process by which complex behavior emerges, and (c) to outline a program for a new modern synthesis for the selection of complex behavior through reinforcement that parallels the early history of evolution through natural selection.

Selection: the Wellspring of Complexity

A selection process consists of three interrelated steps: variation, selection, and retention. Variation provides the raw material upon which selection operates. It is the source of whatever novelty arises from repeated cycles of the three-step process because selection acts only on preexisting entities. Variation itself is undirected: The factors that affect variation are uncorrelated with those that implement selection (Campbell, 1974; although cf. Neuringer, this volume). Selection by the environment favors (or disfavors) some variants over others, and confers to the process whatever direction it appears to display. Selection processes are not directed in a teleological sense, however. The future does not draw the present toward itself, but rather the past pushes the present into the future. The trajectory of selection depends utterly on the environment. If environmental contingencies are constant or change gradually, behavior appears to be adapted to the environment: to display foresight and purpose. This illusion is shattered when environmental contingencies change abruptly. Selection processes prepare us to behave in accordance with past contingencies, not future contingencies except insofar as they mirror the past. The third step, retention, permits favored variations to endure long enough to add to the variation upon which future selections act. Without retention, selections cannot accumulate and the possibility of complexity is precluded. Note that complexity is a possible, not a necessary, outcome of the three-step selection process. (For discussions of the implications of selectionism for behavior, see Catania, 1995, Donahoe & Wessells, 1980, Donahoe & Palmer, 1994, Palmer & Donahoe, 1992, Skinner, 1966, and Staddon & Ettinger, 1989. For more general philosophical treatments, see Dennett, 1995; Hull, 1973; Mayr, 1988; and Sober, 1984.)

Two aspects of a selection process are emphasized here. First, the selecting factors are external to the objects of selection. That is, the environment does the selecting, not the organism. With respect to the selection of behavior, the environment and the organism are partners embraced in an eternal dance, but the environment is always in the lead. The organism is not autonomous. Of course, the organism may influence the course of selection indirectly through the effects of its behavior on the environmental contingencies encountered in the future. However, self control—in any scientifically meaningful sense—first requires acknowledgment of the primacy of environmental control. Paradoxically, the more one reconciles oneself to the primacy of the environment, the more one may truly achieve self-control.

The second aspect of selection is the interdependence of its three steps. As an illustration, consider the relation between variation and retention in the selection of behavior. At birth, the pool of behavioral variation consists of the retained effects of selection by the ancestral environment (e.g., reflexive relations between the environment and behavior) as they are affected by momentary variations in the contemporaneous environment. Following birth, the pool of behavioral variation is rapidly enriched by the retained effects of past selections by the individual environment; i.e., selection by reinforcement. If the contingencies of reinforcement are somewhat variable (i.e., if somewhat different operants are selected in similar environments), the pool of environment-behavior relations enlarges (see Neuringer, this volume). In contrast, if the environment selects only a small number of environment-behavior relations, variation diminishes and, with it, the possibility of complexity (e.g., Schwartz, 1980). Selectionism has triumphed in biology. Darwin's principle of natural selection stands at the heart of accounts of the emergence of complexity from molecules to men. In psychology, however, the situation is different. Among the disciplines that claim behavior as their subject matter, only behavior analysis regards a single principle—the principle of reinforcement—as the central insight into phenomena from conditioning to cognition (e.g., Donahoe & Palmer, 1994) For behavior analysis, the consequences of behavior determine the fate of behavior, whether simple or complex. Some consequences increase the likelihood of a given behavior in an environment, and are termed reinforcers. Other consequences decrease its likelihood, and are termed punishers. A great deal of progress has been made toward formulating a principle of reinforcement that can accommodate a wide range of observations at many levels of measurement (e.g., Baum, 1974; Donahoe, Burgos, & Palmer, 1993: Herrnstein, 1970; Premack, 1959; Rescorla & Wagner, 1972; Timberlake & Allison, 1974; Timberlake & Wozny, 1979; Staddon, 1983). Nevertheless, few psychologists share the behavior-analytic view that reinforcement is fundamental to the emergence of complex human behavior.

Why has a single selection principle triumphed in biology, but languished in psychology? For clues to the answer, it is instructive to examine the events that led to the acceptance of selectionism in biology. Perhaps, comparable circumstances are necessary for the ascendance of selection by reinforcement in psychology.

Parallels with Evolutionary Biology

Natural selection is now accepted as the unifying principle of biology, but this consensus was reached only slowly, and remains controversial within the extrascientific community to this day. Within biology, most of Darwin's contemporaries accepted the general notion of evolution even before the publication of *The Origin of Species* in 1859. That is, they accepted the general proposition that complex species were somehow related to their progenitors. Many of these same biologists, however, rejected natural selection as the overriding explanatory principle. Most believed that natural selection played a role in the production of small changes--varieties within species--but not in what were regarded as qualitative changes between species. Different plumage of pigeons might result from natural selection, but not the larger differences between species, say pigeons and cows. The boundaries between different species--types, kinds, or essences--were regarded as unbridgeable by natural selection (Carpenter, 1860).

For students of behavior, the conceptual counterpart of evolution is individual development. The idea of development--that the child gives rise to the adult--is incontrovertible. Development of

the individual is readily appreciated because, in contrast to the time scale of evolution, it may be detected within the lifetime of a single observer. Psychology, however, faces difficulties that were not encountered by the biologist in the analysis of evolution: Past selections leave no physical record that is readily observable at the behavioral scale of measurement, i.e., there are no behavioral fossils. What endure are such subtle relics as changes in behavior that emerge during extinction (cf. Epstein, 1983) or changes in synaptic efficacies among neurons. And, the latter are legacies that have little, if any, identifiable counterpart at the behavioral level. To observe synaptic changes requires a sophisticated technology that has only recently become available. This state of affairs--together with the intermittency of observations of the entire history of reinforcement of any complex behavior--encourages appeals to developmental discontinuities, to stages of development. Stages are the conceptual equivalents of special acts of creation and are hallmarks of many developmental theories (e.g., Piaget, 1953). Will more complete observations at the behavioral and neural levels reveal that the selecting effect of the environment no more requires the postulation of distinct stages of development than natural selection requires separate acts of creation? I suspect so. Darwin's comment on the incompleteness of the fossil record applies with equal force to the developmental record, "... the more important objections relate to questions on which we are confessedly ignorant; nor do we know how ignorant we are" (Darwin, 1859).

Natural Selection

As noted, the biological community rapidly embraced the notion of evolution, but rejected natural selection as the driving force of evolution. Even Wallace, the coformulator of the principle of natural selection, resisted its application to that most complex creature, man: "Neither natural selection nor the more general theory of evolution can give any account whatever of the origin of sensation or conscious life . . ." (Wallace, 1869). Darwin himself was careful in his early writings to minimize the implications of natural selection for human evolution. The reluctance to apply selectionism to humans was rooted in ideology, not science, as most philosophers and historians of biology agree.

Even the rediscovery of Mendel's experimental work on inheritance was not sufficient for the acceptance of natural selection. Prior to Mendel, Darwin had proposed a so-called blending theory of heredity in which the characteristics of offspring were intermediate between those of its parents. The Scots engineer Jenkin (1867) argued that Darwin's own theory did not meet the requirements of natural selection—rare changes would be overwhelmed by the blending process. Mendel's results were crucial because they implied a particulate theory of genetics in which rare changes would not be obliterated. Mendel's work, however, was not immediately interpreted to support natural selection as the chief engine of complexity. Instead, the discovery of mutations, which critically enhance the variation upon which selection operates, was initially taken to mean that evolution was the result of many special acts of creation (mutations). In addition to Mendel's particulate theory of genetics, something else was needed before the full implications of natural selection could be accepted. The final piece of the puzzle was provided by population genetics. Population genetics is a set of quantitative methods that precisely trace gene flow over time (Fisher, 1930; Haldane, 1931; Wright, 1939). The integration of these methods with experimental work in genetics (e.g., Dobzhansky, 1937; Mayr, 1942) provided a means by which natural selection could be implemented and through which the emergence of

complex species could be understood. This integration is known as the *modern synthesis* in evolutionary biology.

Impediments to Selectionism

What were the ideological impediments to the acceptance of selectionism in biology? Two philosophical precommitments of creationists are generally recognized: essentialism and teleology. (The historical literature cited here was taken from an invited presentation to the American Psychological Association in which modern cognitive psychology was likened to creationism in Darwin's time; Donahoe, 1983.) Each of these factors is examined in turn because they now conjoin to resist selection by reinforcement as the central insight into the emergence of complexity in individual behavior.

Essentialism. Essentialism, in the evolutionary context, was the view that individual variability within a species masked an unchanging entity, or essence, that was the nature of that species. Different pigeons might vary in their appearance, but all pigeons were assumed to be expressions of a common, invariant pigeoness. For the essentialist, the unobservable entity--the species prototype--was what was real. Individual differences merely obscured the true objects of study, the species. More generally, essentialism is the view that the variability inherent in observation is an imperfect reflection of an immutable underlying true reality. Essentialism may be traced to Plato's allegory of the cave. Plato likened efforts to understand the true nature of things to the task confronting an observer who attempts to infer the characteristics of objects casting shadows on a cave wall from the shadows alone. The observer detects only the shadows, not the objects casting the shadows. For the selectionist, the allegory of the cave is fundamentally misconceived. There can be no invariant objects--no essences--because selection processes do not produce static entities. The contingencies of selection imposed by a variable environment are themselves somewhat variable with the consequence that the products of selection processes are inescapably variable. Selection processes constrain the range of variation to a degree that depends on the variation in contingencies (Palmer & Donahoe, 1992; Skinner, 1935). Returning to the allegory of the cave, there are no objects, there are no essences.

The following are essentialist statements from Darwin's contemporaries. With appropriate substitutions of wording, e.g., complex behavior for complex structure, these statements are redolent of the current debate between behavior analysis and normative psychology concerning the role of selection by reinforcement. (In normative psychology, behavior is viewed as an imperfect reflection of unobservable entities--associations, attitudes, cognitions, and the like--that are the true objects of study. These events, however, are inferences from behavior and are not themselves amenable to direct experimental analysis.) The naturalist Wollaston said of the complex structures of living organisms, "Such cases bespeak thought, imagination, and judgment, all and each of the highest stamp, and are utterly inexplicable on any . . . principle of selection" (Wollaston, 1860, p. 133). Sedgwick, a geologist, commented: "What is it that enables us to anticipate the future, to act wisely with reference to a future good? . . . These faculties, and many others of like kind, are a part of ourselves quite as much as our organs of sense" (Sedgwick, 1860, p. 164-165). Or, "How unscientific to trust to an uncertain chance for existence, (rather) than . . . a principle of adaptive creation" (Anonymous, 1860, p. 224). The Biologist Agassiz (1860) held that, "individual differences are 'individual peculiarities,' in no way connected with the essential features of the species" (as cited in Mayr, 1976, p. @). Agissiz

proposed to discover these essential features through what he called *intuition*. (The appeal to intuition is reminiscent of the view of some linguists that insights into the nature of language can be achieved through *linguistic intuition*.) As a final example of essentialism among Darwin's contemporaries, "Self-consciousness [and] reason [require] a representative faculty. . . . Brutes have only the presentative faculty. The faculties of men and those of other animals differ in kind" (Mivart, 1871, p.).

Contrast these essentialist statements with those of the modern biologist, Mayr (1976): "Averages are merely statistical abstractions; only the individuals of which the populations are composed have reality" (p. 28). Or, in the words of one of Darwin's contemporary supporters, "The thing species does not exist; the term expresses an abstraction" (Lewes, 1860). For the selectionist, terms such as *species* in evolutionary biology and association or cognition in normative psychology are instrumental fictions (i.e., they are intended to be theoretically useful, but entail no existential claim). (See the contrast between nominalism and realism in Palmer & Donahoe, 1992; see also Marr, this volume.) To wit, the term species might designate the modal features of a group of individual organisms of common ancestry and, as such, facilitate communication among evolutionary theorists. Consider also the term association. If a learner responds reliably in the presence of a particular stimulus on a number of occasions, the mean latency of the response may be computed. For some purposes, the mean latency may be useful; e.g., for predicting whether a given learner will generally respond faster than another. If, however, the mean value is taken as a measure of an entity that is said to exist within the learner--an association--then the theorist has reified the statistical abstraction. That is, the theorist has conferred existential status upon an abstraction and transformed it into a material or concrete entity: an essence. This error of reification is compounded when the theorist then speaks of the association as causing the behavior from which the entity was inferred: a further error of circular reasoning.

Within contemporary psychology, numerous instances of essentialist thinking are found. For Chomsky and his followers, variability in verbal behavior is thought to obscure underlying universal, language-specific rules (cf. Pinker, 1994). On this view, verbal behavior cannot be selected by the impoverished stimuli provided by the environment. Instead, verbal behavior is seen as the product of a Language-Acquisition Device--an organ of the mind--whose characteristics are inferred from verbal behavior and whose origins are uncertain. There are many difficulties with this proposal (see Catania, this volume; Palmer, 1986, 2000; Palmer & Donahoe, 1992), but the essentialist core of the position is illuminated by comparing Chomsky's views with those of Max Müller, a linguist who was Darwin's contemporary.

When the evolutionists contend that the development of the mind of man out of the mind of an animal is a mere question of time, [I am] inclined to treat the idea with impatience. Animals must be animals as long as they lack the faculty of abstracting general ideas. . . . Mr. Darwin's fallacy lurks in the very word 'development' for the admission of this insensible gradation would eliminate the difference between ape and man. . . . In fact it would do away with the possibility of all definite knowledge. . . . Animals do not possess rational language *because they are not man* [italics added]. (Müller, 1872, p. 145)

From their shared essentialist conceptions of language, some present day linguists deny selection by reinforcement and assert natural selection whereas their predecessors denied natural

selection and asserted creationism. What unites these linguists across the centuries is their common rejection of selectionism--natural selection in M□ller's case and selection by reinforcement in Chomsky's. They have mortgaged their souls to Plato and Kant (Dennett, 1995; cf. Weimer, 1973).

From the outset, behavior analysis was explicit about the variable products of selection by reinforcement as shown in the generic nature of the concepts of stimulus and response (Skinner, 1935). Typically, responding to a somewhat variable set of stimuli with a somewhat variable topography of responses satisfies a given reinforcement contingency. For example, a pigeon might respond to various aspects of the location, shape, or color of the key while striking the key with the beak or other body parts, all of which were followed by a reinforcer. A given reinforcement contingency generally selects a range of environment-behavior relations that differ from one moment to the next and from one organism to the other (cf. Catania, this volume; Reynolds, 1961). Invariant entities—essences—are not produced by selection processes, whether natural selection or reinforcement. (See Palmer & Donahoe, 1992 for a discussion of this issue.)

Teleology. The second ideological impediment to selectionism in biology was teleology. Teleological explanations appeal to events that could occur, if at all, only after the events that they are said to explain. Teleological explanations are inherently essentialist because they postulate the existence of causes that, by definition, cannot exist at the time they are called upon; i.e., before the events they are said to cause. Thus, teleological explanations are essentialist. In biology, an illustration of teleology would be an appeal to a future need to breath on land as the cause of the evolution of lungs in fish. This account requires the fish to know while in water what could be known only later on land. Darwin's critics decried his efforts to understand complexity as the emergent product of what they regarded as the overly simple process of natural selection. Said one critic: "Their whole occupation is to trace every fact to some immediate antecedent cause; and they are so anxious to establish regularity of sequence and uniformity of law, that they cannot bear the idea of a Creator stepping in" (The Patriot, 1863, p. 594 -not in references). And another, "Forces which are not directed--so-called blind forces--can never, so far as I can see, produce order" (von Baer, 1873, p.@). The biologist Huxley, Darwin's ardent supporter, replied that appeals to design "worked not only negative, but positive ill, by discouraging inquiry..." (Huxley, 1908, p.@), a theme echoed in Skinner's much later critique of pseudoexplanations in normative psychology (Skinner, 1950). A modern biologist has summarized the import of Darwin's principle of selection as follows: "Natural selection solved the riddle, how it is possible to produce adaptiveness without the intervention of a goaldetermining force" (Mayr, 1982, p.)

Modern psychology does not appeal to the deity as a goal-determining force, of course. In a selectionist approach to explanation, such locutions are regarded with suspicion lest they conceal a kernel that is not susceptible to the selecting effects of the environment. Natural selection transforms ancestral contingencies into the appearance of design; selection by reinforcement transforms individual contingencies into the appearance of intention.

Although teleology's siren call is most apparent in accounts of complex behavior, traces remain in some modern treatments of even simple behavior. An influential account of Pavlovian conditioning (Rescorla & Wagner, 1972) holds that behavioral change (i.e., learning) requires a discrepancy between the asymptotic associative strength supportable by a given reinforcer and

the net associative strength of all contemporary stimuli that have been paired with that reinforcer. This inference is based on the finding that environmental and behavioral events that precede a putative reinforcing stimulus are unaffected when they are accompanied by another stimulus that was previously paired with the same reinforcer. As an example, suppose that a light was previously paired with food and a tone later accompanied the light when both stimuli were paired with food. If the tone is subsequently presented alone, it does not evoke salivation (c.f., Kamin, 1968, 1969). Prior pairing of the light with food is said to block conditioning to the tone. The phenomenon of blocking is among the most important in modern experimental work. This theoretical formulation of blocking, however, is problematic. Leaving aside the essentialist character of association, the theory postulates the existence at the outset of conditioning of an entity that can exist (if at all) only at the end of conditioning, namely, the asymptotic associative value. Unlike the net associative strength of all contemporary stimuli, which reflects the learner's experience with events in the past, the asymptotic associative value refers to an event that is in the future. For present behavior to be a function of asymptotic associative value, the organism must know from the outset of learning the ultimate strength of association sustainable by the reinforcer. In fact, this formulation requires universal foreknowledge of the asymptotic association strength sustainable by all reinforcers that might ever be encountered (Donahoe, 1984). From whence might such foreknowledge arise, from natural selection? And, if so, foreknowledge must exist for all possible conditioned reinforcers as well. For a selectionist account to be viable, the events that promote conditioning must be physical events that occur in the organism's past or present. In conditioning, these events are restricted to the sensory and behavioral consequences of the reinforcing stimulus and whatever other events are contemporaneous with the reinforcer. The concept of asymptotic association value may provide a useful summary term for the theorist in a description of learning, but its physical counterpart is not available to the learner at the outset of the conditioning process. As indicated shortly, discrepancy may be defined without recourse to teleological and essentialist concepts such as asymptotic associative value (see Donahoe, Crowley, Millard, & Stickney, 1982; Donahoe et al., 1993; Stickney & Donahoe, 1983).

A Possible Counterargument. Let us consider a possible counterargument to the claim that normative psychology and creationism share a deep philosophical kinship. The counterargument runs as follows: Behavior analysis and normative psychology are fundamentally different enterprises. They are so different that it is inappropriate to evaluate them by common epistemological criteria (see Morris, this volume, for further discussion of the relation between behavior analysis and normative psychology). According to this view, reinforcement theory seeks to identify functional relations between observed environmental and behavioral events whereas psychology seeks to characterize abstractly (i.e. in a purely logicomathematical form) the structures and processes that underlie these relations. This purported counterargument recapitulates the two-spheres position in the 19th-century debate between selectionism and creationism about the origin of species (Ellegård, 1958). The two spheres were science and religion (cf. Galuska, this volume). Each was accorded primacy within its respective domain: matter in the first case and spirit, or mind, in the second. Although the modern version in normative psychology bears a fundamental similarity to the two-spheres attempt to reconcile science and religion, few psychologists would accept the explicit dualism of this version of the counterargument.

A more subtle version of the two-spheres counterargument holds that behavior analysis and normative psychology are incommensurate because they seek answers to different kinds of questions, differences in biology that are analogous to the why questions addressed by evolution and the *how* questions addressed by physiology. In this distinction, the evolutionist seeks to identify why (i.e., the selective pressures) a lizard's scale became a bird's feather whereas the physiologist seeks to determine how (the physiochemical mechanisms) the change came about. This more sophisticated version of the counterargument also fails to capture the distinction between behavior analysis and normative psychology. Behavior analysis seeks to answer both how and why questions by recourse to experimental analysis of events in the physical world (observable environmental and behavioral events); psychology, like religion, seeks its answers in the realm of inferred processes. The underlying entities of normative psychology are formalisms that are not defined in ways that permit them to be readily mapped onto the physical world (cf. MacCorquodale & Meehl, 1948). Indeed, some psychologists regard the liberation of theoretical constructs from physiology as one of the most important advances in the field (Mandler, 1981). Note, it is *not* the process of inference per se that is questioned--inference is the starting point of much experimental analysis--but only inferences about entities that cannot, in principle, be subjected to direct experimental analysis.

Evolutionists and physiologists regard the answers to both *why* and *how* questions as informed by selectionist thinking. As an example, consider the neurochemist inquiring into the biosynthetic pathway of a neurotransmitter, a *how* question. Even at the molecular level of analysis, the work is guided by selectionism. Natural selection leads neurochemists to anticipate that biosynthesis will terminate at the earliest possible step in the reaction chain after the target compound has been produced. Termination at the earliest step prevents the synthesis of unnecessary compounds whose metabolic costs would reduce fitness: the answer to a why question. If biosynthesis were found to terminate at a later step in the reaction chain, neurochemists would not reject natural selection. Instead, they would suspect the existence of a previously unrecognized compound that shared a portion of its biosynthetic pathway with the target compound. In short, natural selection is a unifying theme in biology that guides answers to both *why* and *how* questions. *Why* and *how* questions are directed at different parts of the same physical world, both of which are illuminated by selectionist thinking, not at two qualitatively different spheres.

Mayr summarized his analysis of the conflict between Darwinian selection and creationism thus: "No typologist [i.e., essentialist] has ever understood natural selection, because he cannot possibly understand it." (Mayr, 1976, p. 173); "No two ways of looking at nature could be more different" (Mayr, 1976, p. 28). If Mayr's pessimistic verdict applies to the present differences between behavior analysis and normative psychology, little can be gained from the present exploration of the parallels between psychology and creationism. One may hope for the redemption of normative psychology, however, because it can draw upon the Darwinian example of the triumph of selectionism over essentialism and teleology.

A number of signs suggest that normative psychology is evolving in directions consistent with selectionist thinking. First, an intensive analysis of the individual case is becoming more common in psychology, which represents a return to an earlier psychophysical tradition (cf. Uttal, 1999). Selection by reinforcement operates on a population of environment-behavior

relations of a single organism, not a population of different organisms, which is the province of natural selection. Normative psychology has most often taken variation between individuals as its reference population, but this is inappropriate for a science of behavior (cf. Sidman, 1960). The cautions of the cognitive psychologist Hintzman (1980) concerning individual differences in memory illustrate one of the earliest encouraging trends in this direction within normative psychology (see also Neisser, 1982). Second, the logical and experimental pitfalls encountered when structures and processes are inferred from behavioral observations alone are becoming apparent in normative psychology. As but one example, behavioral findings from memory experiments have been variously inferred as indicating that experience is stored as propositions (verbal statements) or as images (perceptions). Many experiments attempted to identify the nature of what was stored, but they met with little success. Anderson's and Townsend's separate refinements of Skinner's (1950) reservations about identifying underlying processes from behavioral observations make this point (Anderson, 1978; Townsend, 1972), as does Hintzman's more general critique of cognitivism (Hintzman, 1993). Problems with identifying processes are particularly troubling because they undermine the falsifiability criterion; i.e., that scientific statements are potentially refutable by evidence. Third, normative psychology increasingly appeals to structures in the real nervous system, not merely instrumental fictions. The increasing appeal to neuroscience in the analysis of complex behavior, as in some instances of cognitive neuroscience, is evidence of this trend (e.g., Gazzaniga, 2000). Appeals to the real nervous system do not guarantee a selectionist approach, of course. Neuroscientists are members of a mentalistic culture and, as such, some recapitulate the errors of Darwin's contemporary critics (cf. Ellegård, 1958, p. 8). A final reason for guarded optimism is that static views of behavioral processes are being replaced by dynamic conceptions (e.g., Galbicka, 1992; Rumelhart & McClelland, 1986). Dynamic conceptions are less prone to essentialist explanations because there are no static entities to serve as surrogates for essences.

The future of normative psychology is much less promising if it persists in the pursuit of explanations that rely on essentialist inferred processes. Although history may applaud contemporary psychology for directing experimental attention toward complex behavior, very little of its theoretical content will endure. In this scenario, normative psychology will make a contribution much like that of Gestalt psychology: Gestalt psychology directed mainstream science toward important and overlooked phenomena, but its specific theoretical proposals are of historical interest only. Encouraging psychology to confront the complexities of human behavior is an important contribution, but much more can be achieved if the analysis and interpretation of complex behavior is informed by the Darwinian example. The modern synthesis in evolutionary biology took over 70 years from the publication of Darwin's *Origin of species* in 1859 to Dobzhansky's *Genetics and the origin of species* in 1937. Will the acceptance of reinforcement as the central insight into complex behavior be similarly delayed, and what must occur for selectionism to triumph in psychology? The final section addresses these questions.

Toward a New Modern Synthesis

To review, the conjunction of three factors resulted in the triumph of selectionism in biology: (a) formulation of a functional principle of selection (natural selection), (b) identification of biological mechanisms that implemented the functional principle (genetics), and (c) development of quantitative methods that traced selection over time (population genetics). (See Table 1). What circumstances obtain in present day psychology?

Requirements for the Acceptance of Selection	in Evolutionary Biology	in Psychology
Functional statement	Natural	Selection by
of a principle of selection	selection	reinforcement
Biological mechanisms	Mendelian	Neuroscience
of selection	genetics	(synaptic plasticity)
Quantitative procedures	Population	Computer simulation
for tracing selection	genetics	(neural networks)

Table 1. Historical parallels between the conditions necessary for the acceptance of selectionism in evolutionary biology and in psychology

Principle of Behavioral Selection

A functional principle of selection by reinforcement is at hand. In the first half of the 20th century, experimental analysis identified the first of two critical conditions: spatio-temporal contiguity with the reinforcer. Whether stimulus-reinforcer relations are studied with the Pavlovian procedure or response-reinforcer relations with the operant procedure, the selected events must occur close together in space and time (Catania, 1971; Grice, 1948). (Several challenges to contiguity remain, however, notably taste aversion in the respondent procedure; e.g., Domjan, 1980; and conditioning with long delays in the operant procedure; e.g., Lattal & Gleeson, 1990.) In the last half of the century, the second condition was identified: discrepancy. As defined at the behavioral level, a discrepancy occurs when the putative reinforcing stimulus evokes a change in ongoing behavior. The two factors of contiguity and discrepancy have been integrated into a functional principle of reinforcement that can be stated as follows: If a stimulus produces a change in behavior, that stimulus functions as a reinforcer, and whatever stimuli immediately precede or accompany the change acquire control of whatever responses immediately precede or accompany the change (Donahoe et al., 1982; Donahoe et al., 1993; cf. Rescorla & Wagner, 1972). This principle applies with equal force to the Pavlovian, or classical, procedure and the operant, or instrumental, procedure. In the classical procedure, the selected

stimulus is the conditioned stimulus (in context) and the selected response is the response evoked by the reinforcing stimulus. Thus, a tone followed by food comes to control salivation. In the operant procedure, another response--the operant--joins the stimulus and response that are selected in the classical procedure. Thus, sight of the lever comes to control lever pressing in addition to salivation when pressing is followed by food. Because of the response-reinforcer contingency that defines the operant procedure, the operant occurs in temporal proximity to the reinforcing stimulus and its evoked response; i.e., to the behavioral discrepancy. In both procedures, food functions as a reinforcer to select environment-behavior relations because food produces a behavioral discrepancy, namely, a change in salivation. As a result, the operant as well as the reinforcer-evoked response is captured by the conditioning process. This account is consistent with Skinner's view that the operant contingency is fundamentally superstitious: Operants need not cause reinforcers to be selected; they need only accompany them (Skinner, 1948).

The foregoing statement of the reinforcement principle provides a basis for unified reinforcement theory (URT). This theory is unified in the sense that it applies equally to conditioning in the Pavlovian and operant procedures. URT is also consistent with Skinner's analysis of punishment (Estes & Skinner, 1941). The account of punishment exploits the implication of URT that conditioning generally proceeds more rapidly for Pavlovian evoked responses than for operants: The evoked response, which occasions the discrepancy, occurs closer in time to the discrepancy than to the operant. That is, because the operant necessarily comes before the reinforcing stimulus by some time interval, the operant is temporally more removed from the discrepancy than the evoked response (see Donahoe & Palmer, 1994, p. 60 and Donahoe et al., 1993, for details). The more rapid conditioning of the evoked response leads to the prediction that a stimulus that evokes behavioral change functions as a punisher when the evoked response is incompatible with the operant. On this account, lever pressing that has been reinforced by food weakens when it is followed by shock because shock evokes escape responses that become conditioned to the sight of the lever and compete with lever pressing (cf. Bersh, Whitehouse, & Mauro, 1982). The operant, however, does not decline in strength as it would with an extinction contingency in which the operant occurs but is no longer reinforced. The punishing stimulus does not directly weaken the operant but, instead, escape responses interfere with the operant and thereby prevent its further occurrence. The suppression of lever pressing eliminates further pairings of lever pressing with food and thereby precludes the possibility of extinction. When the punishing contingency is removed, the operant may recover much of its strength after escape responses have extinguished.

Another implication of URT is that when reinforcer-evoked responses are compatible with the operant, the operant strengthens especially rapidly. Thus, food-reinforced pecking by pigeons is readily acquired because pecking both precedes the reinforcing stimulus and is evoked by it. The observation that pecking reflects both the operant contingency in the location toward which the peck is directed and the reinforcer-elicited response in the topography of the peck is consistent with this account (Jenkins & Moore, 1973).

Finally, URT implies that aversive stimuli that would normally function as punishers can serve as reinforcers under some circumstances. To wit, if the operant is compatible with the responses evoked by the aversive stimulus, then the operant may be strengthened by the aversive

stimulus. In confirmation of this prediction, when shock is intermittently made contingent on escape responses, escape responses continue indefinitely--and, consequently, so do presentations of the aversive stimulus (Burns & Donahoe, 1984). The aversive stimulus of shock evokes escape responses and, therefore, shock functions as a reinforcer for operants of similar topography when shock is contingent upon their occurrence. (See Morse & Kelleher, 1977, for a summary of the initial work in this area.)

Unified reinforcement theory, and other moment-to-moment accounts of reinforcement, can be reconciled with reinforcement principles that describe molar relations between variables, such as between responses and reinforcers in the matching relation (e.g., Baum, 1973, 1974; Herrnstein, 1970; but see Davison & Baum, 2000). In the matching relation, the relative frequency of an operant approximates the relative frequency of reinforcement for that operant. It has been shown that dynamic (i.e., moment-to-moment) accounts of reinforcement may yield this molar relation as their cumulative product under some circumstances (e.g., Shimp, 1969; Staddon, Hinson, & Kram, 1981; see also Donahoe, 1977). Thus, moment-to-moment accounts of reinforcement need not be inconsistent with the molar relations between variables found after prolonged exposure to the contingencies of reinforcement.

Biological Mechanisms of Selection by Reinforcement

A functional principle of natural selection is important for understanding evolution apart from the genetic mechanisms that implement it. Similarly, a principle of reinforcement based on behavioral observations is critical to understanding complex behavior apart from its biological mechanisms. Nevertheless, if the Darwinian parallel holds, the general acceptance of reinforcement as the central insight into complex behavior may depend upon identifying the mechanisms that implement it. Note that the motivation for seeking the biological mechanisms of reinforcement is pragmatic, not epistemological. That is, an understanding of reinforcement based only on behavioral observations may be logically sufficient, but politically unpersuasive (cf. Schaal on reductionism, this volume).

Behavioral justifications also exist for seeking knowledge of the biological mechanisms of reinforcement. Some stimuli evoke behavioral changes (thus satisfying the definition of a behavioral discrepancy), but do not function as reinforcers. For example, an increase in the ambient light level causes the pupil to dilate, but a tone paired with the increase in light does not come to control dilation. In contrast, electric shock evokes papillary dilation and does function as a reinforcer under otherwise comparable conditions (e.g., Gerall & Obrist, 1962; see Donahoe & Wessells, 1980, pp. 114-115 for other examples). Thus, the production of a behavioral discrepancy is not invariably an occasion for reinforcement. Conversely, some stimuli produce no readily apparent behavioral change (thus not satisfying the discrepancy requirement), but nonetheless function as reinforcers. For example, many conditioned reinforcers evoke little responding but, nevertheless, such reinforcers play a critical role in the acquisition of complex behavior. Thus, reinforcer-evoked responses do not always provide a reliable measure of the ability of a stimulus to function as a reinforcer. Finally, a purely operational definition of reinforcers as stimuli that increase the probability of the behavior on which they are contingent encounters difficulties in its generality. A stimulus that functions as a reinforcer for one response may not function as a reinforcer for a different response (e.g., Shettleworth, 1972); a stimulus that functions as a reinforcer for one organism may not function as a reinforcer for other

members of the same species because of differences in their experiences (as in blocking); and a stimulus that functions as a reinforcer at one time may not function as a reinforcer at a different time for the same organism (as in variations in the state of deprivation) (cf. Meehl, 1950; Michael, 1993). An operational approach can be expanded to include reinforcement history and state variables among its prerequisites, but the foregoing cases suggest that a comprehensive theoretical treatment of reinforcement will draw upon the experimental analysis of neuroscience as well as behavior.

When behavior analysis began in the early 1900s, neuroscience was more a promise than a reality. Consequently, neuroscience could contribute little to understanding selection by reinforcement (see Skinner, 1938; Thorndike, 1903; see also Donahoe, 1999). The present state of affairs is different, however. Behavioral research has now identified the events that appear critical for reinforcement and new technologies in neuroscience increasingly permit the neural, cellular, and genetic accompaniments of reinforcement to be experimentally analyzed (for some examples, see Schaal, this volume). Although Skinner viewed the experimental analysis of behavior as "a rigorous, extensive, and rapidly advancing branch of biology" (Skinner, 1974, p. 255), he was equally clear that neuroscience was a different branch of biology. Although the two fields are independent enterprises, they are also interdependent in the same sense as other biological subdisciplines; e.g., neuroscience and biophysics. Under the working hypothesis that the acceptance of selection by reinforcement will parallel the acceptance of natural selection, what follows is a brief overview of the biological mechanisms of reinforcement. Special emphasis is given to the relation between these mechanisms and findings from the behavioral analysis of reinforcement.

Behavioral research has demonstrated that the environmental guidance of behavior is extremely flexible: almost any environmental event can control almost any behavior. How do the biological mechanisms of reinforcement accommodate this fact? Neuroscience indicates that reinforcement at the cellular level is dependent on compounds called *neuromodulators*. Axons from the cells that liberate neuromodulators project widely throughout the brain. Thus, neuromodulators can alter many synaptic efficacies simultaneously and permit almost any sensory input to control almost any motor output.

Unconditioned reinforcers, such as food, stimulate receptors that ultimately cause cells in the midbrain to liberate a neuromodulator (dopamine). Behavioral research indicates that reinforcers select environment-behavior relations only when these events occur close together in time: the contiguity requirement (Catania, 1971; Grice, 1948). When a presynaptic neuron firesultimately, because of the occurrence of an environmental stimulus--it liberates a transmitter (glutamate) that stimulates two types of receptors on a postsynaptic neuron-fast receptors and slow receptors. If fast receptors are sufficiently stimulated, the postsynaptic neuron fires. In addition, short lasting structural changes (tags) are produced in the stimulated fast receptors. Further, if the fast receptors are stimulated for a sufficient duration, slow receptors also become engaged. Finally, if the reinforcer-instigated neuromodulator is present at about the same time that the slow receptors are engaged, a series of intracellular events take place that produce long-lasting structural changes in the tagged fast receptors. These changes cause fast receptors to undergo long-lasting increases in their sensitivity to the neurotransmitter liberated by the presynaptic neuron. (For experimental support for the preceding statements regarding the cellular

mechanisms of reinforcement, see Frey, 1997; Stein & Belluzzi, 1989; Stein, Xue, & Belluzzi, 1993). This increased sensitivity is known as *long-term potentiation*. The net outcome of the process is that the neuromodulator potentiates multiple synapses between coactive neurons along the neural pathways that mediate reinforced environment-behavior relations. In this way, stimuli that precede the reinforced response come to control behavior.

In addition to the contiguity requirement, the discrepancy requirement established by behavioral research also has its neural counterpart: Reinforcing stimuli, including conditioned reinforcers, increase the release of the neuromodulator from cells in the midbrain only if those cells have not been activated recently. To illustrate, the ingestion of food normally increases the firing of these midbrain cells. If food, however, is preceded by a stimulus such as a light that has been previously paired with food, food no longer causes the liberation of the neuromodulator. Hence, food is rendered ineffective as a reinforcer under these conditions. Instead, the light now produces an increase in firing of the neuromodulator cells and, hence, functions as a conditioned reinforcer (Schultz, 1997). The inability of food to increase the firing of dopamine-producing neurons is responsible for the behavioral phenomenon of blocking (cf. Donahoe, 1997). Much remains before the neural mechanisms of reinforcement are fully known, but the correspondence between the contiguity and discrepancy requirements identified by behavioral research and the cellular requirements identified by neuroscientific research indicates that a comprehensive account of reinforcement is approaching.

Quantitative Means for Tracing Behavioral Selection

Finally, what progress is being made in the development of quantitative techniques to trace the effects of selection by reinforcement? Are there methods in the offing that do for reinforcement what population genetics did for natural selection? The implications of natural selection and reinforcement can be illuminated by other than quantitative means, but if the Darwinian parallel holds, purely verbal accounts will not be fully persuasive, even within the scientific community. In addition, both behavior analysis and neuroscience increasingly appreciate that exploring the cumulative effects of basic processes may be too complex to pursue through experimental analysis alone. Complex behavior is the result of a complex history of reinforcement that is often impossible to duplicate in the laboratory. The difficulties are particularly formidable with nonlinear processes, such as occur in the nervous system: With nonlinear processes, two systems that behave identically under the same circumstances do not necessarily react identically when exposed to the same future circumstances (e.g., Smolensky, 1986). To model the effects of selection by reinforcement, a promising technique uses computer simulations of networks of neuron-like units. These simulations employ learning algorithms to modify the strengths of connections between units in a manner that is consistent with behavior analysis and neuroscience (e.g., Donahoe et al., 1993; Donahoe & Palmer, 1994; Donahoe, Palmer, & Burgos, 1997). To model the effects of natural selection on neural networks, a related type of computer simulation employs genetic algorithms to develop architectures of neural networks in a manner that is consistent with genetics and developmental neurobiology (e.g., Burgos, 1997).

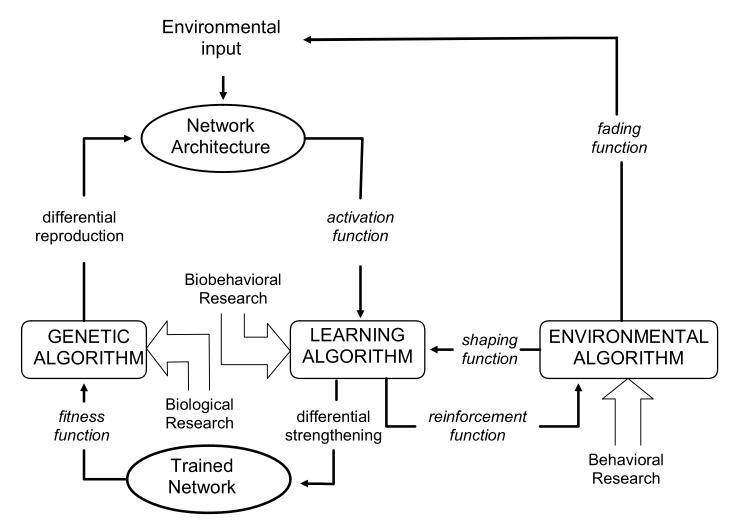


Figure 1. Overview of a comprehensive selectionist approach to the interpretation of complex behavior using computer simulations. The process begins with the stimulation by the simulated environment of inputs to a network architecture (an artificial neural network). The network architecture is a product of a genetic algorithm. The genetic algorithm simulates the effects of natural selection and neurodevelopmental processes on network architecture. A learning algorithm then modifies the strengths of connections between units in the neural network, thereby simulating selection by reinforcement. An environmental algorithm specifies the stimuli that provide inputs to the artificial neural network (the fading function), the response topography that is required for reinforcement (the shaping function), and the consequences that occur for various topographies of response (the reinforcement function). After the strengths of connections have been modified by the learning algorithm, a population of trained networks is formed. These networks differ from one another in their performance subsequent to the simulated contingencies of selection. The differences in performance are reflected in differences in the "fitness" of the networks. Repeated cycles of the selection process simulate successive "generations" of natural selection and selection by reinforcement. (See Donahoe, 1997.)

The figure provides an overview of a comprehensive selectionist approach to the interpretation of complex behavior by means of computer simulation. The process begins with stimulation by simulated environment inputs to a network architecture (an artificial neural network). The network architecture is a product of a simulated genetic algorithm. The genetic algorithm simulates the effects of natural selection and neurodevelopmental processes on the differential reproduction of network architecture. The environmental input to the network architecture functions to activate a learning algorithm. The learning algorithm then modifies the strengths of connections between units in the neural network, thereby simulating selection by reinforcement. An environmental algorithm specifies the stimuli that provide inputs to the network architecture (the fading function), the response topography that is required for reinforcement (the shaping function), and the consequences that occur for various topographies of response (the reinforcement function). After the connections have been differentially strenthened by the learning algorithm, a population of trained networks is formed. These networks differ from one another in their performance following the simulated contingencies of selection. The differences in performance result in differences in the *fitness* of the networks to the contingencies. Repeated cycles of the selection process simulate successive generations of natural selection and selection by reinforcement. (See Donahoe, 1997.)

As with experimental analysis, the interpretation of selection processes can be carried out at different scales of measurement. Simulations can model the selection of environment-behavior relations at the behavioral level (Hutchison, 1997), and at the biobehavioral level--the selection of synaptic efficacies that mediate operants (e.g., Donahoe & Palmer, 1994; Donahoe et al., 1993). Similarly, simulations can model the synaptic level (e.g., Hasselmo & Wyble, 1997) or the neurochemical level (e.g., Smolen, Baxter, & Byrne, 2000). Whatever the level of the simulation, quantitative techniques must be constrained by findings from independent experimental analyses (see arrows in Figure indicating the influence of behavioral, biobehavioral and biological research). For example, within a neural network, a given unit (the analog of a neuron) cannot have direct excitatory effects on some units and inhibitory effects on others: A single neuron in the nervous system does not liberate both excitatory and inhibitory neurotransmitters. The need to be constrained by findings from experimental analysis distinguishes biobehaviorally acceptable quantitative methods from superficially similar methods in normative psychology such as parallel distributed processing (Rumelhart & McClelland, 1986). These latter simulations are primarily constrained by logical and mathematical considerations (cf. Donahoe & Palmer, 1989), not by experimental science. Ultimately, quantitative methods that draw upon experimental analyses from different scales of measurement must be integrated to provide a comprehensive theoretical account as depicted in Figure 1 (see also Donahoe & Dorsel, 1997).

Conclusions

Selectionism holds that complex phenomena are products of a three-step process acting over time. First, variation occurs in the phenomena that are subject to selection. Then, selection unequally favors some of these variations. Finally, retention of the selected variations allows them to contribute to the pool of variation upon which later selection operates. The products of selection are themselves necessarily variable because variations in the contingencies of selection are inevitable. In principle, then, the product of a selection process cannot be a constant entity, or

essence. Essentialism regards variations in phenomena as merely perturbations of an underlying, unchanging entity. Because of this inherent difference in their views of the nature of phenomena, selectionism and essentialism are fundamentally irreconcilable.

In evolutionary biology, selectionism won the day after an almost 100-year struggle against two philosophical obstacles: essentialism and teleology, essentialism's frequent companion. In normative psychology, camouflaged forms of essentialism persist in the guise of entities such as associations, attitudes, cognitions, linguistic rules, and the like. Experimental observations are seen as imperfect reflections of underlying relatively fixed structures or processes whose characteristics can be inferred from the variable observations. By contrast, behavior analysis accepts the variation in observations as irreducible—even under circumstances that meet the rigorous demands of experimental analysis—and seeks to induce principles that accommodate variation. Chief among these principles is a principle of reinforcement, which describes the processes that select behavior. Behavior analysis views a well-conceived principle of reinforcement as playing the same role in the understanding of complex behavior that natural selection already plays in understanding the evolution of complex organisms.

The triumph of selectionism in biology was principally due to the formulation by Darwin of the principle of natural selection. A functional statement of the principle of natural selection, however, was not sufficient for its acceptance. General acceptance awaited the discovery of the biological mechanisms that implemented natural selection and the development of quantitative procedures that traced its implications. The conjoining of these enterprises is known as the *modern synthesis*. Behavior analysis, critically supplemented by experimental findings from studies conducted within the conceptual framework of associationist psychology, appears to have identified a powerful functional statement of the principle of reinforcement. Although this functional statement may be logically sufficient to provide an account of the emergence of complex behavior, it may not be adequate for the acceptance of selectionism in psychology. If the fate of selectionism in psychology parallels its course in evolutionary biology, the biological mechanisms of reinforcement must be discovered and suitable quantitative techniques must be devised before most will find the account persuasive. The rate of progress in both of these enterprises encourages the belief that a new modern synthesis is emerging over the horizon.

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