The Convergence of Behavioral Biology and Operant Psychology: Toward an Interlevel and Interfield Science

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Behavioral biology and operant psychology have developed in parallel but separate paths since their origins in the 1930s. In the first three decades, both fields dealt with microscopic (or molecular) controlling variables and qualitative data. Since about 1960, both have primarily focused on macroscopic (or molar) controlling variables. Their shared interest in foraging in the 1980s suggests a limited convergence beween biologists and psychologists in data, methods, and theories. We draw on accounts of intertheoretic relations from the philosophy of science, including both interlevel theory and interfield theory, to understand this convergence. However, our greater emphasis on methods of data collection and analysis leads us to characterize the convergence as not only one of interfield theory but one of interfield science.

　Key words: ethology, behavioral ecology, optimal foraging theory, evolutionary theory, interfield theory, history of behaviorism

There has been more change of late in behavior analysis than either the public or even most psychologists are aware. Contrary to rumors of the demise of general behavioral laws through the discovery of autoshaping and other "biological constraints," the scientific community referred to as "the experimental analysis of behavior" has engaged, since the 1960s, in the successful confirmation of newly-discovered quantitative laws based on immensely refined methods of investigation. Its theories and methods bear only a distant relationship to the operant psychology of the four schedules and the single pigeon key-peck chamber described in most textbook introductions to psychology. Our purpose is to sketch some developments in the neighboring fields of behavioral biology and operant psychology and to characterize the degree of their convergence.

I. TOWARD AN ANALYTIC FRAMEWORK OF INTERFIELD SCIENCE

Since the 1930s, theory reduction has been the hallmark of the philosophy of science. Biological and psychological explanation, it was argued, could be subsumed under lower levels of explanation involving physico-chemical laws (Nagel, 1961). Thus, the deductive-nomological model proposed "covering laws," patterned after the syllogism, for predicting what would happen under certain hypothesized testing conditions (Hempel, 1966).

With the advent of the new history of science in the 1960s, philosophers of science turned more and more to actual case studies to understand the nature of scientific progress (e.g., Laudan, 1977; Nickles, 1973). The more philosophers considered the actual process of scientific discovery, the more they began to loosen their classical notions of rationality based

on deductive-nomological laws and hypothetico-deductive procedures. One among many promising attempts to come to terms with science as it actually progresses is called interfield philosophy.

According to interfield philosophers, a scientific field contains the following (Darden & Maull, 1977, p. 44):

A central problem, a domain consisting of items taken to be facts related to that problem, general explanatory factors and goals providing expectations as to how the problem is to be solved, techniques and methods, and, sometimes, but not always, concepts, laws and theories which are related to the problem and which attempt to realize the explanatory goals.

Notice the breadth of this description of a field. While scientists are inclined to emphasize theoretical differences between fields, interfield philosophers instead emphasize their theoretical agreements and overlaps. Indeed, they focus on hybrid concepts and mechanisms that grow out of the interrelations between fields. Importantly, the hybrid conceptual vocabulary is that actually employed by scientists.

A second feature of interfield science, one which we perhaps emphasize more than philosophers of science, involves methods and techniques. Philosophers have traditionally given short shrift to actual scientific methods in their emphasis on rational reconstructions of science. Even Darden and Maull emphasize theory, including intertheoretical relations, to the neglect of method. We will give special emphasis to experimental techniques, types of data, and styles of analysis. In this respect, we extend their definition of a field somewhat. We will show, for example, how operant methods involve certain kinds of recording devices that have been extended to allow the measurement of naturally occurring behavior. As for classical ethology and optimal foraging theory, they use comparative behavioral research to describe and order "the action systems of phylogenetically related species" (Lorenz, 1950/ 1971b, p. 130). The initial descriptive phase of research is followed by a systematic one.

Third, it is important before we proceed to acknowledge that one of the characteristics of fields, their explanatory goals, remains far apart for the fields of ethology/behavioral biology, on the one hand, and operant psychology/quantitative analysis on the other. Evolution means different things to these different fields. Ethology, for example, uses homologies, or comparisons between behavior patterns of two related species, in order to draw phylogenetic conclusions (Eibl-Eibesfeldt, 1970; Lorenz, 1941/ 1971a), while operant psychology simply assumes a phylogenetic contribution to the present behavior of the organism (Schwartz, 1984). Be this as it may, we shall bear in mind that our convergence between fields may be limited by some major divergences in explanatory goals.

Whatever the qualifications in the nature of the convergence we shall investigate between two fields, we believe that we have here a powerful analytic framework, one which is not just philosophical but historical as well. It can help us to understand the type and the degree of interfield convergence, and divergence, between existing fields. Thus, we submit this as a case study to join other case studies in the sciences, each one different and illuminating in its differences (cf. Bechtel, 1986a). To mention just one of the classic cases of interfield science, the operon theory of molecular genetics posited the physical control of enzymes involved in patterns of inheritance; allosteric regulation accounted for enzyme catalysis through structural changes in proteins. These two theories brought together biochemistry and genetics, physical chemistry and biochemistry (Bechtel, 1986b, 1988; Darden & Maull, 1977).

In a prescriptive sense, interfield theory can tell us what to look for in the nature of any science. As a descriptive tool, it serves to raise our awareness of the components of any scientific endeavor. One spokesperson for integrating scientific disciplines remarked that "even when two disciplines work on a common problem area, they may have different ways of investigating that domain and

interpreting their results" (Bechtel, 1986, p. 13).

We want to alert the reader, moreover, to the relation between interfield and interlevel theory (McCauley, 1986). We use the term *level* to characterize a shift from molecular variables to molar variables, both independent and dependent. Thus, we trace a shift vertically *between* levels, as well as horizontally between fields. But we do not necessarily mean replacement of one level by another, since the initial level continues to grow alongside it.

Consider an historical example from another discipline. During the early 1900s, the microlevel of gene theory seemed incommensurable with the macrolevel of large-scale variation in mutations. By the 1920s, however, chromosomal genetics had described a source of variability on which selection could occur at the population level (Bechtel, 1986a; Darden, 1988; Darden & Maull, 1977).

Using our example of an interlevel and interfield theory, the operant explanation of foraging behavior need not be reducible to classical contiguity-based behavioral principles of reinforcement; and conversely for biologists, the explanation of species-typical behavior need not be limited to the operation of discrete releasing stimuli during critical periods. Instead, both operant psychology and behavioral ecology have developed nonreductionist interlevel accounts of complex behavior. Moreover, this is also an interfield situation in that these two fields can complement one another. Scientists have drawn upon problems, experimental techniques, and even theories and models from one field and reapplied them in their own areas.

In what follows, therefore, we will talk about more than theory or even intertheoretic relations. We attempt to build upon the philosophers of science insofar as we show changes in the nature of theory within the disciplines of biology and behavior analysis over the past half century. But we extend our historical discussion beyond theory to include other elements of science, such as laboratory and naturalistic methods, the kinds of data from each, and the phenomena which constitute the variables in the respective fields.

II. FROM ETHOLOGY TO BEHAVIORAL ECOLOGY

Recent literature reviews (Gray, 1987; Krebs, Stephens, & Sutherland, 1983; Pyke, 1984; Schoener, 1987) claim that behavioral ecology has become a dominant field in the biological study of animal behavior, coming to overshadow the field of ethology in the past half century. We will focus on a subarea of behavioral ecology called *optimal foraging theory* (hereafter OFT), whose primary concern is feeding. We admit that the realm of behavioral ecology extends beyond feeding to include areas such as reproduction, communication, and social behavior (Krebs & Davies, 1981). Two chronological periods may be distinguished.

Ethology, 1930 to 1960

Ethology was the dominant field from the 1930s through the 1960s in behavioral biology (Gould, 1982). Two characteristics of present interest define the classical ethology of Konrad Lorenz near Munich, Niko Tinbergen and Eibl-Eibesfeldt at Cambridge, J. L. Gould at Princeton, and Peter Klopfer at Duke University (e.g., Lorenz, 1965, 1971c). First, they offered *qualitative* descriptions of species-typical behaviors. The data are described qualitatively in the sense that no numbers are assigned to observations, and no predictions are offered. Instead, classical ethologists cataloged naturally occurring behavior patterns for each species in an ethogram consisting of innate releasing mechanisms, fixed action patterns, and species-typical behavior. Second, they explained species-specific behavior by *molecular* variables. For example, in the imprinting of young birds to their mothers during critical periods, discrete releasing stimuli were found to operate during a relatively short "critical period" (Hess, 1973). Other well-known examples of what we term

molecular variables cited by ethologists are the release of aggressive or mating behavior by the particular color of the stickleback's belly (Tinbergen, 1952), the dance language of bees (Frisch, 1971), eggshell removal from the nest (Tinbergen, 1963), or the step-by-step mating activities of ring doves (Klinghammer & Hess, 1972). Descriptive studies of such behavior appeared predominantly in the European journals *Behaviour, British Journal of Animal Behaviour, Auk,* and *Zeitschrift für Tierpsychologie.*

Classical European ethology remained to a considerable extent a field apart from mainstream American behaviorism, even while sharing a common interest in objective accounts of behavior. But it had a very serious explanatory goal: namely, by observing behavior patterns in related species, to find those which correspond; these they called homologies (Lorenz, 1941/1971a, p. 19). Correspondence indicates a common phylogenetic origin of instinctive behavior patterns. To the classical ethologist, it is obvious that counting responses in just one domain, such as feeding—as learning psychologists did in pursuit of general laws of learning—is to limit oneself to ontogenetic, and therefore incomplete, evidence. Instead, ethologists preferred to use a substantial number of homologous and analogous characters to make their case for or against phylogenetic homology, or common descent. Thus, ethologists treated behavior patterns as phenotypic characters, subject to natural selection.

Optimal Foraging Theory, 1960–1980

Research based on optimal foraging theory differed from classical ethological research in respect to two of its defining characteristics. OFT drew on mathematical models developed by population ecologists and behavioral biologists (e.g., Charnov, 1976a, 1976b; Emlen, 1966; Krebs, 1973; MacArthur & Pianka, 1966; Royama, 1970; Schoener, 1971). Its work appeared in such outlets as *Journal of Animal Ecology, Theoretical Population Biology, American Naturalist,* and *Animal Behavior.* Thus, OFT is *quantitative,*

beginning with complex mathematical models that demand numerical data rather than descriptive data. Second, OFT postulated control over behavior by *molar* variables. Behavior occurs over the long term, and behavioral biologists chart average effects over periods in which animals would encounter various types of prey and different places to forage.

The new field also served to identify and open up further areas for study. Early mathematical formulations in the field of optimal foraging predicted behavior patterns that maximized energy intake over a given period of time. This energy metabolism model was loosely derived from the experimental physiology of nutrition. For example, Charnov (1976a) suggested that animals would choose between different food types in an order that yielded the highest rate of energy intake. Later, Charnov (1976b) proposed another model, the marginal value theorem, predicting that animals would choose places to feed that would similarly maximize energy intake.

While the ethology of the pre-1960 period did employ the concept of adaptation, it could not readily include the concept of maximization. The specification of an optimal behavioral pattern demands precise, quantitative description of behavioral and environmental elements. The qualitative and molecular paradigm of the classical ethologists offered little toward the precise deduction of optimal strategies. Ethologists thus identified some important general principles, but also compiled a large catalog of facts about species-typical behavior that required organization. Thus, the field of OFT required methods and theories lacking in classical ethology. This problem caused advocates of OFT to become interested in operant technologies and methods.

The advantage of the concepts of maximization and optimality developed in behavioral ecology was that these were general principles applicable to the species-typical behavior of many kinds of animals. OFT, while contriving to observe significant samples of naturally occurring behavior, broadened the classical approach by claiming that principles

governing the natural feeding patterns of different species—that is, efficient behavior produced by natural selection—were now susceptible to quantitative description in molar terms.

Interlevel is reflected in the juxtaposition of empirical observation of species-specific behavior in the wild and theoretical extrapolation from population models. Missing, however, was a technique of measuring naturalistic behavior with sufficient precision to test the elaborate mathematical models. OFT would surely benefit from closer attention to the catalog of species-typical patterns, and particularly sequences of "fixed-motor patterns" described so well by classical ethologists. We shall now consider how classical operant psychology and quantitative operant psychology have met some of these needs.

III. FROM OPERANT PSYCHOLOGY TO THE QUANTITATIVE ANALYSIS OF BEHAVIOR

So far, we have described only developments in behavioral biology, especially the emergence of behavioral ecology, entailing a major shift in research emphasis from field observation to mathematical modeling. An analogous shift has taken place independently within operant psychology, based on evidence from reviews by Davison and MacCarthy (1988), Fantino and Logan (1979), Nevin (1984), and Wearden and Burgess (1982).

Operant Psychology, 1930–1960

In retrospect, we can characterize Skinner's operant paradigm from about 1930 to 1960, like ethology, as qualitative and molecular. Skinner gathered qualitative data primarily in the form of cumulative records of responding using analogue recorders; he described his data in terms of scallops, slopes, and plateaus (Ferster & Skinner, 1957). In the early years, he toyed with quantitative formulas, but never posited a general law (Coleman, 1987). He, unlike the dominant psychologists in animal learning, was not

willing to employ the techniques of mathematical modeling. He argued that the mazes which Hull and Spence used did not yield data of adequate precision to allow testing of their mathematical models. As broad as was Skinner's vision for behaviorism, it was rooted in a single organism, counting approach to quantification rather than in more abstract mathematical relationships. Indeed, the cumulative record seemed by design to rule out hypothetical entities and inferred constructs, including mathematical ones (Smith, 1986, p. 305). In addition, we want to emphasize that a response for Skinner was a *class* of many different activities grouped together by a common reinforcing consequence. An operant was not a single movement; many different movements could produce the same reinforcer and therefore be defined as the same operant.

Skinner also specified the independent (controlling) variables for behavior in *molecular* terms. Reinforcers comprised proximate events whose action occurred at the local level of discrete but repeated encounters. The three-term contingency (the response, the reinforcer, and the discriminative stimuli) was treated as a *functional* unit, similar to the way ethology treated fixed action patterns as a functional unit. Thus, the action of reinforcers, like releasing stimuli, was contiguous. This was the original paradigm of Skinner, presented in book form in 1938, definitively summarized in *Schedules of Reinforcement* (Ferster & Skinner, 1957), and centrally represented in the *Journal of the Experimental Analysis of Behavior* at the time of its founding in 1958. It is also the prevailing view of operant psychology taught to undergraduates in textbooks up to the present time (for an exception, see Brown and Herrnstein [1975]).

Quantitative Analysis of Behavior, 1960–1980

A new field has emerged from operant psychology, however, since the early 1960s. Like behavioral ecology, it is both molar and quantitative, and it draws from other fields to predict new relations in

these domains. By virtue of its embracing predictions and mathematical models, the field of the experimental analysis of behavior has expanded to include an explanatory, theoretical science in addition to a descriptive, Baconian one (cf. Smith, 1986).

When Herrnstein studied at Harvard in the early fifties and returned there to join the faculty in the late 1950s, he combined S. Smith Stevens' interest in mathematics with the operant psychology of Ferster and Skinner. Then Herrnstein took over primary responsibility for the pigeon laboratories, while Skinner turned his attention elsewhere. Herrnstein's research explicitly generated mathematical functions describing relative responding to two or more concurrent alternative contingencies. This marriage of quantitative with empirical behavioral science was extended by members of the Harvard laboratory in the 1960s, including William M. Baum, Shin-ho Chung, Edmund Fantino, Philip N. Hineline, Peter Killeen, Howard Rachlin, Bruce A. Schneider, Richard Schuster, and John Staddon. Herrnstein and his protegés collected and analyzed data in a new way, shifting their attention from cumulative records to digital counters and from absolute to relative measures of responding (Baum, 1973; Baum & Rachlin, 1969; R. J. Herrnstein, personal communication, 1988; Herrnstein & Hineline, 1966; Killeen, 1968). Skinner's cumulative records were graphical in the sense of describing behavior using time and cumulative response coordinates. Herrnstein's analyses were graphical in a different sense of mapping a function or fitting a line to the data points.

This work retained Skinner's concept of the operant, and the single organism emphasis. But mathematical precision in the definition of stimulus, response, and reinforcement contingencies meant that, as Herrnstein later reported, "we found functional relationships on a par in reproducibility and generality with those of psychophysics, then psychology's most advanced field" (1987, p. 449). From the point of view of interfield theory, the mere introduction of more precise methods and

standards of measurement allowed for an interlevel shift from molecular to the molar independent variables, dependent variables, and reinforcement contingencies.

For example, in the 1960s the Harvard laboratory also defined a mathematical relationship between responding and reinforcement in an equation that has been called the *matching law* (Herrnstein, 1961, 1970, 1974). This equation described the relative allocation of behavior to various alternative activities as a matching process, measuring relative rates of reinforcement for each activity. As in behavioral ecology, behavior and reinforcement were both molar variables, that is, they were averaged from large numbers. In short, the matching equation suggested that one had to situate any single behavior pattern in the context of other behavioral alternatives. The action of reinforcement on patterns of behavior was global rather than local, and integrated over many response-reinforcer encounters during long periods of time.

Thus, this new research left behind the cumulative record and contiguity-based molecular analysis in favor of concurrent and multiple schedules and relative response rates. By varying overall rates of reinforcement, the experimenter could obtain corresponding changes in response rates. These molar relations were orderly, and did not require underlying, more reductionistic explanations.

IV. PRELIMINARY CONVERGENCE OF BEHAVIORAL BIOLOGY AND THE QUANTITATIVE ANALYSIS OF BEHAVIOR SINCE 1980

During the past decade, convergence has occurred on two fronts. Behavioral biologists have used the experimental technology of behavior analysis, including the operant chamber and digital recording devices, to generate controlled quantitative data (Lea, 1979, 1981; Redhead & Tyler, 1988; Ydenburg, 1984). Operant researchers, meanwhile, have conducted experiments with the explicit

goal of testing optimal foraging models (Baum, 1983; Hineline & Sodetz, 1986; Mellgren, 1982; Mellgren, Misasi, & Brown, 1984). In other words, the field of behavioral ecology has obtained more of its data from operant instrumentation, while the experimental analysis of foraging has modified and extended mathematical models from biology.

Consequently, predictions now run in both directions. Sara Shettleworth (1988), John Staddon (1981), and George Collier and Carolyn Rovee-Collier (1981) have presented a new view of behavior, both inside and outside the experimental chamber. Their approach regards operant behavior inside the experimental chamber as foraging, and foraging in the wild as operant behavior. They are psychologists who have made overtures to ecologists. If this hybrid approach went further in the assimilation of technique and theory, we could look for truer interfield convergence in which methodologies from different fields are brought to bear on a common problem.

Links to Evolutionary Theory

For operant psychology, this shared instrumentation and models have already established modest linkages to evolutionary thought. These linkages are still under construction, and they constitute a further interfield effort. Operant psychologists have always known that behavior analysis must utilize concepts of variation and selection of behavior, and that it must take into account phylogenetic as well as ontogenetic mechanisms (Baum, 1983; Staddon, 1983; Staddon & Simmelhag, 1971). So far, the matching law and marginal value theorem hold promise as accounts incorporating both proximate and ultimate causal mechanisms. What behavior analysts need from the behavioral biologists and ecologists are natural histories of behavior and a greater understanding of population ecology and species differences.

Fantino (1985) has argued that by viewing operant behavior in the context of foraging, we can extend principles developed in the operant conditioning lab-

oratory to natural domains in the wild. This allows direct connections to evolutionary theory by specifying proximate mechanisms (such as his delay reduction hypothesis), as well as general approaches to behavior (such as optimality or systems theory). Such theoretical formulations would reach beyond the proximate controlling mechanisms studied traditionally by operant psychologists to encompass the effects of more distal events in both the ontogeny and phylogeny of the species (Baum, 1983; Staddon, 1983).

The convergence of these subfields of biology and behavior analysis represents in some respects a natural extension of what Skinner proposed in his ambitious program to situate operant psychology within the biological sciences. Skinner directly addressed evolutionary matters in "The Phylogeny and Ontogeny of Behavior" (1966), and later in "The Shaping of Phylogenic Behavior" (1975), "Selection by Consequences" (1981), "The Evolution of Behavior" (1984), and "The Evolution of Verbal Behavior" (1986). However, these theoretical essays for the most part follow the more technical developments in the field by a decade or two. And empirical work, data testing, and mathematical models are not yet explicit in Skinner's suggestive ideas. It is others who have incorporated molar operant ideas, as well as mathematical models, to yield evolutionary conclusions. To some extent, Skinner has become the popularizer of a movement which some of his disciples have taken in new directions.

Toward an Interfield Behavioral Science

From another perspective, of course, a shift of major proportions has occurred. For decades prior to 1960, psychologists who studied animal behavior in the laboratory and biologists who studied animal behavior in the field had little common discourse. But since the late 1970s, as indicated by three joint interdisciplinary conferences on foraging, they have begun to form new alliances (Commons,

Kacelnik, & Shettleworth, 1987; Kamil, Krebs, & Pulliam, 1987; Kamil & Sargeant, 1981). Not only have they achieved consensus on quantitative and molar dimensions of the study of behavior, but they have defined principles such as the matching law and the marginal value theorem which may, with future modification, help to establish an interfield behavioral science.

Meanwhile, in the last several years, behavioral biologists have been expanding their conceptual framework to include ideas and techniques from operant psychology. They have begun rethinking one of their underlying assumptions, namely, that of optimality (Gray, 1987). To this end, they have exploited the precision of operant techniques to refine their own formal models. For example, some have used operant signal detection techniques to study prey detection by blue jays (Kamil & Yoerg, 1982; Yoerg & Kamil, 1988). Behavioral ecologists acknowledge the quantitative models of neo-operant psychologists such as Herrnstein, Fantino, and others in their foraging papers (e.g., Stephens & Krebs, 1986). Here, the assumption appears to be that behavioral biology has the ecological models and descriptive tools to better study ultimate causes, while experimental analysis can better sharpen the quantitative description. With this natural division of labor, the two subdisciplines have begun to embrace one another.

Interlevel and Interfield Theory of Behavior

The convergence we have described comprises several levels of theory and a variety of research techniques. During the period from 1930 to 1960, ethologists relied on molecular observations of instinctive behaviors and early experimental behavior analysts studied operant units strengthened by repeated but contiguous response-consequence encounters. They employed naturalistic observation and cumulative records obtained in highly controlled laboratory settings. One field sought to account for imprint-

ing of a stimulus presented during a critical period, while the other measured learning through multiple stimulus presentations and reinforcement. However, the theories of both were qualitatively descriptive rather than quantitative. It is no wonder, given the differences between their methods and goals, that these two fields had little contact.

During the ensuing period of 1960 to 1980, the traditional focus of both fields on lower-level molecular relations expanded to include higher-level molar relations. One of the reasons for the crossing of disciplinary boundaries at this time had to do with increasing sophistication of scientific instrumentation (e.g., introduction of digital recording devices driven by computers) and acceptance of mathematical modeling as a legitimate enterprise. Ecologists had had problems measuring naturalistic foraging, and thus they came to employ operant technology. The predictive features of mathematical models from population ecology could now be combined readily with the operant technologies for counting responses. Another common goal inspiring the convergence, it would seem, was the description of both the ontogeny and phylogeny of behavior. Psychological researchers from Darwin to Skinner have stated this goal, but have not fully realized it, in large part because of the lack of organizing laws to relate behavior to phylogenetic and ontogenetic environmental conditions.

Above all, therefore, it is equations such as the matching law which seem to hold promise for bridging the fields of the experimental analysis of behavior, the physiology of energy metabolism, population ecology modeling, and classical economics. Here are mathematical formulas with empirical validity, which behavioral biologists and behavioral psychologists alike can test across many species.

We have traced a limited convergence of at least two fields, behavioral ecology and operant psychology, over the past six decades. During the first three decades, the fields shared a molecular and a qualitative approach to data collection and

theory; during the second three decades, they evinced a molar and a quantitative approach. These parallels in themselves suggest at least a limited convergence, whereas in fact we have shown that they were far apart in the 1930s and have only begun to converge in the 1980s. Certainly we do not yet have an interfield theory joining them, though existing variants of the optimality laws point to one relating their findings to evolutionary theory. Of more profound historiographical significance is the very idea of examining recent science in the terms used here, terms encompassing technique and method, theory and laws, persons and communities, and of course, historical trends.

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