

*EVOLUTION, BEHAVIOR PRINCIPLES, AND DEVELOPMENTAL SYSTEMS:
A REVIEW OF GOTTLIEB'S SYNTHESIZING NATURE-NURTURE:
PRENATAL ROOTS OF INSTINCTIVE BEHAVIOR*

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Gottlieb's developmental psychobiology book provides a base for reexamining the place of the experimental analysis of behavior in the life sciences. His experimental program demonstrating the critical function of the environment in the development of a species-typical behavior helped force an acceptance of probabilistic epigenesis, the acknowledgment that the developmental genome-environment system is fully interactional. (Indeed, nature vs. nurture is deader than a doornail.) The repercussions for evolutionary biology and the roles and categorizations of genes, behavior, and environment in behavior-environment relations are explored in light of current knowledge, including specific implications for the experimental analysis of behavior.

Key words: Nature-nurture issues, developmental psychobiology, probabilistic epigenesis, evolution, behavior categories, genes, imprinting

Almost a century ago, Zing-Yang Kuo joined John B. Watson in challenging prevailing ideas about instincts. Watson researched both "instincts" and learning, and claimed a large role for the environment in behavior. Kuo showed that what had been thought to be fully genetically determined "instincts" depended on environmental factors. For example, cats raised with rats did not attack them or other adult rats (Kuo, 1930). In a different field, Driesch had found environmental influences at a different level when a two-celled sea urchin embryo with one cell excised developed into a normal adult. The environment of the cell—that is, whether it was attached to another cell or not—altered its developmental course. Thus, adult parts are not all present from the start (preformationism), and genes do not simply cause development to unfold in a fixed manner with the environment in a supportive but strictly subsidiary role ("predetermined epigenesis," Gottlieb, 1997). Instead, bidirectional influences are present at all levels, and the environment determines phenotype in a fully interactional partnership with genes, a process Gottlieb named *probabilistic epigenesis* (1970; see also Gottlieb, 1997, 1998). In this

review, I examine the relationships between probabilistic epigenesis, development, evolution, and behavior principles.

The ideas of both Watson and Kuo had been viewed as radical and ignored or decried by many. But Kuo, like Watson, lived to see his ideas celebrated by those who would be his successors; and, in a direct passing of the torch in the 1960s, he trained Gottlieb in the techniques of bird behavioral embryology. Gottlieb then helped end the nature versus nurture dichotomy with his impressive program of research on the malleability of duckling auditory imprinting. Differences in species-typical behaviors might, he showed, be due to the actions of the environment during development as much as genetic differences, rendering expressions like "genetically determined" misleading at best. A particular allele (gene form) leads to a corresponding outcome only in a "normal" environment.

In *Synthesizing Nature-Nurture*, Gottlieb traces the ideas of probabilistic epigenesis, alternating between historical and theoretical commentary and the behind-the-scenes progress of his research line (see also a shorter but more recent version, Gottlieb, 1999). He concludes with the sweeping implications of the findings: a new "modern synthesis" of biology and psychology as evolutionary and developmental sciences, consistent with the old one of Darwinian theory and Mendelian genetics, but greatly expanded in scope (see Bateson, 1988, also cited in Gottlieb; Wcislo, 1989; West-Eberhard, 1989). This view of evolution grants behavior as well as "nurture"

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their rightful places as key players. Learning researchers who have not followed these developments will find a new perspective on the life sciences.

In achieving this goal, Gottlieb ranges across key topics in developmental biology and psychobiology, including spontaneous motility, experimental embryology, genetics, early environmental complexity, perceptual development, songbird song learning, and, on the larger plane, general evolutionary biology and systems theory. But the major empirical focus is on the classic ethological topic of imprinting.

Nature-nurture relations, and their evolutionary context, are of importance for all life scientists, including learning researchers. Despite considerable progress in the understanding of these relations, genetic determinism and other misreadings of nature-nurture relations are still common, even within psychology and biology (Gottlieb, 1997, 1998). The consequences can be serious (e.g., Gould, 1981). Other relevant topics suggested by Gottlieb's coverage include the implications for the scope and categorization of operants and respondents. While learning researchers have successfully elucidated many behavior principles, an understanding of how they relate to developmental and evolutionary principles is still in its infancy.

Although Gottlieb's (1997) valuable research, commentary, and citations are the basis for this review, I have expanded his coverage, especially that pertaining to behavior categorization. All citations originally found in Gottlieb's book are listed as such in their first appearance, and all references to Gottlieb are to his 1997 book, unless otherwise noted.

This review begins with a section describing developmental psychobiological discoveries about the role of the environment ("The Many Functions of the Environment"). A discussion of the potential involvement of operant and respondent principles follows, with the implications for behavior categories ("The Puzzle of Behavior Categories," "The Fate of General Principles of Learning"). Gottlieb's other main topic of interest to learning researchers is covered in the section "Evolution and Behavior." Possible physiological mechanisms behind probabilistic epigenesis are outlined in "Mechanisms and In-

teractions." Finally, "Expanding Horizons" discusses how learning researchers can benefit from the breathtaking advances in these interdisciplinary areas, and how they can contribute to them. But first, a summary of Gottlieb's imprinting results.

GOTTLIEB'S IMPRINTING RESEARCH

The Method

"Species-typical behaviors" have often been called "instincts," "released behaviors," "fixed action patterns," and "species-specific behaviors." Little or no learning is evident in their production; instead, presentation of the appropriate stimulus during a "sensitive period" at the appropriate developmental stage results in the appearance of the behavior.

Determination of the provenance of a species-typical behavior like imprinting has been accomplished using the isolation or deprivation experiment, in which subjects are given no opportunity to learn the skill components under investigation. For nest-building, for example, young birds might be prevented from seeing nests or nesting material until their arrival at breeding age. If these birds are then immediately able to build a nest successfully, nest-building does not depend on these sorts of experiences.

Manipulation of food or other objects, however, could have been essential. It is difficult to completely rule out such "nonobvious" environmental contributors (Gottlieb, p. 76; West, King, & Freeberg, 1994, also cited in Gottlieb). For example, monkeys that were fed live insects developed a fear of snakes; without the live insects, the fear did not occur (Masataka, 1994, also cited in Gottlieb). A lack of alternative methods means experimentation throughout development, including prenatally, is necessary to investigate thoroughly the potential role of "nurture." Gottlieb's careful work exemplifies this approach.

Birds are especially suitable for prenatal studies because embryonic manipulations and measurements are easier than with mammals. Kuo's (1921) suggestion of a role for prenatal experience has been amply confirmed over the years (also cited in Gottlieb; see Schlinger, 1995 for references on human prenatal learning). And Gottlieb's research

has extended that role, testing the limits of environmental influence and the behavioral plasticity of imprinting.

Essential Environmental Contributors

The Nobel prize-winning work of Konrad Lorenz on waterfowl imprinting suggested that vision was the key sensory modality: Hatchlings normally followed their mother during the sensitive period, but in her absence would follow other objects, including Lorenz himself. Once imprinted, the stimulus was thought to be unchangeable and effective for a lengthy period of time, but later work has shown substantial malleability (Bolhuis, 1991; Michel & Moore, 1995, also cited in Gottlieb).

Gottlieb's program also revealed unexpected results, with an immediate finding that auditory imprinting occurred earlier than, and could take precedence over, visual imprinting (but see Bolhuis & van Kampen, 1992). After determining which aspects of the wood duck maternal call were critical, he showed that previous experience hearing siblings' alarm vocalizations was essential for the development of species-typical maternal call preference. In mallards, maternal repetition rate was the important feature, and hearing their own or siblings' calls prenatally at their normal repetition rates and frequency ranges was required for normal maternal auditory imprinting.

These findings appear to resemble simple stimulus generalization. Gottlieb's effective early stimuli sometimes shared few apparent properties with the maternal call, however, and tests found that the maternal call was in any case preferred postnatally over the critical prenatal or perinatal vocalizations. Thus, stimulus generalization did not appear to be a sufficient basis for auditory imprinting.

Malleability

Malleability is demonstrated when the normal preference for the maternal call changes, and it could be shown in both species under the right circumstances. Surprisingly, even a decreased incubator temperature causes non-species-typical imprinting in vocal mallards (Gottlieb, p. 27). (Devocalization would seem to be required because in the earlier work only ducklings that did not hear themselves failed to develop the normal preference.)

Species-atypical preference also can be induced when the ducklings are in social groups, even when the normal mallard embryonic contact calls are presented with the alternative, heterospecific maternal call both pre- and postnatally. Gottlieb determined that tactile contact in the social groups was critical, to the point that isolated ducklings raised with stuffed toy ducklings would, like the socially reared ducklings, prefer the alternative call over the mallard call. Physiological arousal in isolated ducklings without tactile contact reduced this malleability, resulting in normal or no preference. These findings illustrate the caution necessary in generalizing from laboratory results: Raising ducklings in isolation allows more control, but can produce artifacts (see also Michel & Moore, 1995). (Gottlieb observed imprinting in the wild, but he does not discuss the naturalistic imprinting studies or their accompanying criticism of lab research; see Fantino & Logan, 1979; Miller, 1988, also cited in Gottlieb.)

Malleability is just as striking in wood ducks. Early stimulation by wood duckling distress calls is normally necessary *and* sufficient for the development of an appropriate maternal call response. When the distress calls were presented with an alternative stimulus perinatally, however, imprinting occurred to the alternative stimulus.

Despite such unexpected malleability, the developmental systems producing species-typical behaviors normally work adequately for the continuation of the species, and natural selection is conservative. The possibility of change offered by any behavioral malleability, however, is significant on a long-term view, and will be discussed in the "Evolution and Behavior" section.

Commentary

This brief and simplified outline does not do justice to the challenges of this research. Gottlieb is evaluating intricate relations, and close attention is necessary at times to follow the logical sequence as he successively eliminates possibilities. Indeed, a final summary of the findings would have been helpful: The normal auditory imprinting sequence in these waterfowl is a complex function of the type of stimulation, its timing, the duration of contact, and contextual variables; the full details are still being sought. A glossary of

terms also would have been useful to help reach an interdisciplinary audience.

Group designs are necessary for this research, but Gottlieb did look at individual data in some cases (e.g., p. 122). Not every bird was tested for follow-ups, a possible minor methodological concern. As for other concerns, some speculations lack strong support, such as the interpretation given to Glickman and Sroges (1966, also cited in Gottlieb). Also, Gottlieb's Razran (1971) reference is out of date (see Hall & Suboski, 1995). Finally, the book is sometimes repetitious, perhaps reflecting its origin as a series of lectures.

But these concerns are minor. Gottlieb's empirical program was groundbreaking in providing detailed experimental evidence for probabilistic epigenesis. Gottlieb also takes full opportunity to discuss the implications of this and related lines of work.

THE MANY FUNCTIONS OF THE ENVIRONMENT

Gottlieb lists three categories of environmental influences on the development of species-typical behaviors: *induction* (canalization and malleability), *facilitation*, and *maintenance*. (Unfortunately, these terms have not always been used consistently.) Both forms of induction characterize a change that otherwise would not occur. Canalization reduces the scope of responsiveness to stimuli, thus limiting effective releasing stimuli to those that share certain key features. Malleability, the opposite form of induction, expands which features will be effective. Facilitation accelerates an inductive change, but is not essential for the change; and without maintenance, the established behavioral relation decays. Distinguishing between these processes is sometimes difficult (Michel & Moore, 1995), and Gottlieb also does not address the issue of how these forms of environmental effect are related to classical and operant conditioning (see Shettleworth, 1994, who considers this process classification orthogonal to a procedurally-based classification). Behavior categories will be discussed in the next section.

Gottlieb's findings illustrate with two waterfowl species the range of induction possibilities only in imprinting, but similar effects are not hard to find in other species. For exam-

ple, lovebirds will accept and raise young only of the same down color as that of their first hatchlings. If a first brood of other-colored young is substituted, birds will later abandon their own young (Dilger, 1962). Indigo buntings' navigational "star maps" are established by early experience: Whichever star is the stationary center about which the other stars revolve serves as the North Star, even if it is in the south (Emlen, 1970). In many species, sexual imprinting appears to be based on early filial imprinting (Fantino & Logan, 1979; Owens, Rowe, & Thomas, 1999; Witte, Hirschler, & Curio, 2000; but see Bolhuis, 1991). For mallard males, cross-fostering (rearing not performed by parents) produces atypical sexual imprinting, but only for somewhat similar parental-substitute species (e.g., geese, not chickens; summarized in Fantino & Logan, 1979).

The ecological context is important (see section below on Evolution and Behavior). Young male white-crowned sparrows, for example, must hear the adult song to develop the normal song pattern (Snowdon & Hausberger, 1997). But, given the simultaneous presence of songs of many songbird species, malleability such as that demonstrated by Gottlieb for imprinting could easily result in the learning of the wrong song (and occasionally does, e.g., Grant & Grant, 1997). Rather strong canalization is necessary in such contexts, because songs that depart too far from the normal pattern would not be recognized by females or rivals. Indeed, other songs that *are* perceived during the sensitive period are usually ineffective.

Neither the limitations of sensory systems nor learning history can account for these induction examples, although such mechanisms can account for some other "biological constraints" (see Damianopoulos, 1989; Schwartz, 1974; Staddon, 1983). Instead, the developmental genome-environment system is the source. But, of course, this system is ultimately the source for all behavior. How do operant learning and classical conditioning fit in?

THE PUZZLE OF BEHAVIOR CATEGORIES

A fairly common tripartite classification scheme separates species-typical behavior/re-

action chains/tropisms and their cousins from reflexes, habituation/sensitization, and classical conditioning from operant learning in all its forms. But interactions and relations between these proposed phenomena and processes have long been evident, and a major source of speculation (e.g., Dinsmoor, 1985; Domjan & Galef, 1983; Hebb, 1949; Hoffman & Ratner, 1973; Johnston, 1981; Shettleworth, 1993; Suboski, 1990). Even within associative learning, perhaps the most common conclusion is that operant and Pavlovian procedures are separable, but operants typically entail the presence of respondents (Catania, 1998; cf. Donahoe & Palmer, 1994). They certainly share similarities with each other and with species-typical phenomena (e.g., Avital & Jablonka, 2000; Fantino & Logan, 1979). A comprehensive review cannot be presented here, but some of the highlights of species-typical similarities to associative learning will be discussed, plus a brief comment on the involvement of gene-environment interactions. The section below entitled "Evolution and Behavior" includes additional relevant considerations.

Consequences

Initial exposure to a species-typical releasing stimulus can be an operant establishing operation (Catania, 1998). Indeed, some releasing stimuli, like some eliciting stimuli, function as reinforcers, whether natural or contrived—and not only those that serve appetitive-type functions (e.g., rivals, for Siamese fighting fish, as in Hogan, 1967; Lattal & Metzger, 1994; Melvin, 1985). Some of the stimuli for tropisms, common in "simpler" animals, might also be reinforcers (see Teitelbaum, 1977).

In species-typical songbird song learning, the model song can be a reinforcer (ten Cate, 1994). In some species, individuals must hear their own songs following the sensitive period of exposure to models, and adjustments then take place (Staddon, 1988). Might the sensitive period exposure establish a particular song as a reinforcer (canalization/discrimination) so that the bird's attempts to match the song are selectively maintained? Closer matches might thus be automatically reinforcing (Staddon, 1988).

An imprinted stimulus can successfully reinforce a variety of operant behaviors that

produce it, in addition to that of simply following the stimulus (e.g., Bateson & Reese, 1968; Peterson, 1960). Bateson and Reese (1969) found a correlation between the imprinting and reinforcer effectiveness of a stimulus. And the "responsiveness" of the imprinted object or figure may be important, especially when operantly contingent—as in humans with artificial attachment objects (Main, 1999; for nonhumans, see, e.g., ten Cate, 1989; but cf. ten Cate, 1994). The unresponsive objects or figures sometimes used as unnatural imprinting stimuli, however, can function as reinforcers—and without necessarily being imprinted (Gaioni, Hoffman, DePaulo, & Stratton, 1978). Indeed, the reinforcing effectiveness of simple stimulus change appears to play a role in imprinting (van Kampen, 1996).

This effect of stimulus change may be present at birth, a function of prenatal gene-environment interactions. Motivation research that is sufficiently interdisciplinary to incorporate developmental psychobiology and operant research is necessary to determine the variables affecting consequence effectiveness—so essential for understanding operant behavior. This work may be essential for understanding imprinting and other species-typical processes as well.

Finally, such behaviors of species-typical origin can sometimes be operantly modified. Conspecific reactions provide direct operant consequences for song variation in many species (Kroodsma, 1988; Marler, 1991; Staddon, 1988; West, King, & Freeberg, 1994, 1997; see Snowdon & Hausberger, 1997 for other chapters that cover the latest research on the complexities of this subject).

Antecedents

Antecedent stimulus principles offer their own set of parallels. The releasing stimulus itself can resemble an elicitor that is effective only during certain developmental or seasonal periods. Species-typical behaviors can occur without a specific releasing stimulus, however, and, like operants, may include more variability at the molecular level than do respondents (e.g., Hebb, 1949). Given the initial presentation of a releasing stimulus, species-typical behaviors may occur immediately, just as unconditioned stimuli often immediately elicit unconditioned responses. But op-

erant learning and classical conditioning can, under the right circumstances, also occur rapidly. Moreover, species-typical behaviors like imprinting are sometimes a function of experience with the releasing stimulus (e.g., Shettleworth, 1994).

How similar are the characteristics of operant stimulus control, species-typical releasing stimuli, and conditioned and unconditioned stimuli? Phenomena such as that of supernormal stimuli, in which more intense releasing stimuli have enhanced effects, illustrate the limits of canalization even in normal, naturalistic development. The resemblance to respondent stimulus control is clear, and Staddon (1983) noted a similarity to operant peak shift. Other standard generalization effects occur in species-typical behaviors, in common with operants and respondents (e.g., Hoffman & Ratner, 1973). Generalization characteristics can be due to either or both differential learning experience and the "unlearned" side of the developmental genome-environment system as discussed by Gottlieb.

As has been shown throughout, unexpected malleability can occur in species-typical relations. ten Cate (1994) summarized research suggesting that an element of variability in the stimulus or stimulus presentation may enhance imprinting, and possibly species-typical songbird song learning as well. Young white-crowned sparrows may learn the song of a different species from a live model rather than a concurrently presented but taped conspecific song; moreover, the normal sensitive period can sometimes be greatly extended (Michel & Moore, 1995; Staddon, 1988; see also Miller, 1988; Snowdon & Hausberger, 1997).

Sensitive Periods

A variation on standard sensitive periods is illustrated by female hunting wasps that are sometimes capable of modifying the amount of food they bring for their larvae. After a wasp's daily inspection visit, if researchers substitute larger or smaller larvae, the wasp will simply provide whatever she has brought. If the substitution is made prior to the inspection visit, however, the right amount of food will be brought (summarized in Fantino & Logan, 1979). Similarly, Staddon (1983) summarized research on bees showing that

certain foraging discriminations can be learned only at certain times in the foraging sequence (but cf. Couvillon, Leiato, & Bitterman, 1991). Evolutionary flexibility, building on what is available, can seemingly produce almost any behavioral form for any ecological niche. (And the building blocks of species-typical behaviors are still plain to see, even without fossils to study; the range of courtship rituals in the balloon flies is one of the more intrinsically appealing and little-known examples, Evans, 1968.)

The presence or absence of a sensitive period may simply imply a quantitatively but not qualitatively different neural basis (Greenough & Schwark, 1984; cf. Hogan, 1994). The same presumably applies for reflexes such as those restricted to human infancy. The flexibility now apparent in species-typical sensitive periods indicates that even the quantitative differences can be smaller than once thought. Indeed, some researchers consider that there is no true sensitive period for imprinting, but that the process itself brings on its close (e.g., Bolhuis, 1991). Illustrating the behavior categorization problem, however, pigeons' "imprinted" solar navigation does appear to have a sensitive period, but the established behavior is then readily modifiable (Wiltschko & Wiltschko, 1998).

Genes

Clearly, there are still many more questions than answers; and manipulating genetic variables adds another layer of complexity. One of the more advanced interdisciplinary areas involving associative learning, genetics, and developmental processes is that of early environmental complexity. Hebb (1949) reported that rats raised as pets performed better in mazes than normally reared laboratory rats. Cooper and Zubek (1958) then found that more complex environments had no effect on Tryon's "genetically maze-bright" rats, but improved performance for the "maze-dull." Conversely, impoverished environments had little effect on "maze-dull" individuals, but were detrimental for "maze-bright" (see also Kempermann, Brandon, & Gage, 1998; but see Miller, 1988, on some pitfalls of selective breeding research). This range of effects may simply represent the extremes of normal development (Greenough & Sirevaag, 1991; note also the possibility of

ceiling and floor effects). Some of the later studies suggest that further operant involvement in the complex environment may be an essential feature over mere motor activity (Black & Greenough, 1991). Physiologically, more complex environments can increase the complexity of brain (and only brain) RNA, as well as general brain mass and number of synapses, with correlated increases in behavioral capabilities (e.g., Rosenzweig, Krech, Bennett, & Diamond, 1968; Uphouse & Bonner, 1975, also cited in Gottlieb; see Gottlieb, pp. 91, 96).

Many areas of research require similar analyses. Reminiscent of Cooper and Zubek's (1958) study, nature-nurture research using the spontaneously hypertensive (SHR) rat strain has shown that non-SHR maternal care prevents the pups from becoming SHR, but normal rats do not become hypertensive when raised by SHR mothers (Cierpal & McCarty, 1987, also cited in Gottlieb, p. 97; see also Suomi, 1999). What behavioral processes are involved?

Biological Preparedness

The many interactions of nature and nurture that are now evident add to the already apparent intricacies of behavior-environment relations. Changing perspectives on "biological preparedness" over the last 40 years reflect this enhanced understanding.

As seen earlier in this section, imprinting itself appears to entail elements of associative learning (see also Bolhuis, 1991; Shettleworth, 1998; Suzuki & Moriyama, 1999; van Kampen, 1996). As Shettleworth (1993) commented, progress in understanding imprinting recalls the changing views of taste aversion learning, once thought unique and now considered a standard associative preparation, one more malleable than initially thought. Species-typical behaviors like imprinting have also proven to be more malleable than expected. Similarly, operant learning-set ability was once considered a function of evolutionary "phyletic level" among vertebrates, but has been demonstrated in rats (Slotnick, Hanford, & Hodos, 2000; Slotnick & Katz, 1974; see also Shettleworth, 1998).

The concept of "biological preparedness" was proposed to account for those differences in ease of learning that were based on genetic predispositions. From the research described

in this review, no possibility can remain of quantifying preparedness in any straightforward way. Instead, one is reminded of the complex interactions in the developmental genome-environment system that determine the changing level of plasticity of behavior-environment relations (e.g., Spear & Rudy, 1991). Perhaps the biological constraints idea has come to be out of favor because of the increasing recognition of this complexity (Damianopoulos, 1989; Domjan & Galef, 1983; McNally, 1987; see also Schwartz, 1974; Staddon, 1983); any perceived constraints can originate in ontogeny as well as in phylogeny. But preparedness may still be a useful concept in some form (Mineka & Cook, 1995; see also Papaj & Prokopy, 1989), depending in part on what physiologists and developmental psychobiologists like Gottlieb find, in conjunction with learning researchers.

Categorizing: Science Proposes, Nature Disposes

Is there a continuum of behavioral processes or, alternatively, somewhat-fuzzy-but-generally-demarcatable behavior categories appropriately based on operational or procedural distinctions? Only one thing seems clear: The hopes for easy distinctions between species-typical=phylogenetic versus learned=ontogenetic, which psychologists and biologists alike used to think was the case (e.g., Schwartz, 1974), have been dashed forever. Instead, Verplanck (1955) had it right in his *Psychological Review* title: "Since learned behavior is innate, and vice versa, what now?"

THE FATE OF GENERAL PRINCIPLES OF LEARNING

Many different behavioral mechanisms may exist, some specialized and some general, and they may shade into one another (e.g., Domjan & Galef, 1983; perhaps analogous to memory mechanisms, Shettleworth, 1993). But Bitterman (2000) noted "General-process theory is often thought to be contradicted by *adaptive specialization*—the alleged evolutionary tailoring of learning processes to the needs of particular species in particular situations—although the assumption of tailoring implies the existence of general processes to be tailored . . ." (p. 65). And nothing

ing can alter the established finding that, behaviorally, basic operant and respondent principles do appear similar across many species (even invertebrates, e.g., Bitterman; Davis, 1986; Fantino & Logan, 1979). Many other learning principles that are well-studied in rats and pigeons have yet to be investigated thoroughly in other species or in naturalistic settings—even, for example, an apparently ubiquitous phenomenon of great practical importance: matching. Some have argued that general process approaches have failed (e.g., Davey, 1989), but this conclusion seems unwarranted.

On the physiological side, evolutionarily early mechanisms of learning and their genetic bases may not have been conserved; at the least, these early mechanisms must have been substantially altered. In some cases, convergent evolution may have occurred instead. The discovery of the homeobox genes for developmental regulation, however, may be encouraging for the general principles idea. “The finding that every animal has similar genes, has them in the same chromosomal order, and uses them to specify the same relative positions along the anterior-posterior axis” has led to wholesale reevaluation of the evolutionary analogy-homology dichotomy (Gilbert, Opitz, & Raff, 1996, p. 364, also cited in Gottlieb). And the homeobox domain may not be the only genetic “Rosetta stone” (Gilbert et al., p. 364). Although the proteins produced by similar genes can serve different functions, the same genes found in fruit flies and humans are sometimes similar, even identical, in function (Weiner, 1999). Identical, gene-encoded hormones and neurotransmitters exist across many species. Indeed, evolution teaches us that all species must be related—and fully half of the banana genome is present in the human genome (Lander, 2001). Perhaps the genetic basis of learning was itself preserved across untold generations (see, e.g., Papini’s reminder of the possible role of cAMP across species as diverse as molluscs and rodents, even bacteria). Even if a comparable set of genes exists for some learning processes, the physiological mechanisms would not necessarily be identical. Still, similarities clearly do exist for closely related species, and may exist across larger phylogenetic distances.

Similarities in behavior-environment rela-

tions exist across categories, as has been shown. Even Gottlieb’s two forms of developmental induction, canalization and malleability, are analogous to discrimination and generalization in some ways. Once the basic stimulus control and behavior-consequence mechanisms were available for one function, they became available for others, like any other genetically-influenced feature, and could be modified in the process. But general principles may have continued to apply. For example, the capacity for behavior change through reinforcement and punishment evolved early on, and at some point consequences became effective for modifying behaviors other than those that normally produced them (as discussed earlier for imprinting stimuli as reinforcers; see general discussion in Iversen, 1984; species-typical behaviors can interact, Breland & Breland, 1961). Variability itself became a reinforceable characteristic of behavior (e.g., Page & Neuringer, 1985). Such enhanced flexibility eventually enabled the complexities of human behavior. Donahoe and Palmer (1994) suggested that human language is in part a result of greater sensitivity to conditioned reinforcement.

Whether dealing with phenomena best viewed as continua or discrete categories, learning researchers have acted on the assumption that general principles of learning exist, and the larger context of behavioral biology challenges us to test the limits of that assumption. Ultimately, the larger context for any life science is, of course, evolution. What role does behavior play?

EVOLUTION AND BEHAVIOR

Natural selection pressures promote adaptiveness (enhanced “fitness,” meaning survival and reproduction; see Dawkins, 1982), although not all evolved features are adaptive (e.g., Logue, 1988). Learning researchers tend to think of operant learning and classical conditioning as major forms of environmental influence on behavior, and their importance in many species is clear. Reflexes and species-typical behaviors that are released under appropriate circumstances without what can be a risky learning delay, however, have their own advantages and selection pres-

tures (see also Avital & Jablonka, 2000; Stadon, 1983).

The degree and type of environmental input into the large variety of behaviors depend on the happenstance of evolutionary mechanisms, which can produce everything from learning of great flexibility to unlearned tropisms and interesting combinations. The phenotype is the subject of evolutionary selection pressures, regardless of which alternate genetically-supported route produced it (West-Eberhard, 1989). The results can be surprising, as even aspects of insect ovipositing and nectar feeding can depend on learning (Papaj, 1986; Papaj & Prokopy, 1989; in some cases, age-dependent, Wardle & Borden, 1985; see also Wilcox & Jackson, 1998, on operant hunting behavior in spiders). Gottlieb's results also give emphasis to the impossibility of estimating the extent of behavioral plasticity based solely on the form of the phenotype.

The more available developmental malleability or behavioral plasticity, the more likely that species subpopulations will find themselves exploiting new niches, with an enhanced possibility of subsequent speciation. And, although the genome does clearly set limits (as does the environment), the range of possibilities not requiring genetic change is great (Kuo, 1976, also cited in Gottlieb). Developmental genome-environment systems that support plasticity of some sort are generally selected over nonplastic forms, even in simpler organisms (West-Eberhard, 1989). Many species have alternative morphological as well as behavioral phenotypes (West-Eberhard, 1986), both of which can spread faster than genetic changes. Gottlieb and others have long noted that phenotypic changes can thus occur without any changes in the genotype, although those often follow (Avital & Jablonka, 2000).

Only a small proportion of the genome is actually expressed in most organisms (e.g., birds can develop teeth under the right circumstances, Kollar & Fisher, 1980, also cited in Gottlieb, p. 83; West-Eberhard, 1986). Further, no relation appears to exist between genome size and complexity of organism or number of neurons. Salamanders and algae have the most nucleotide pairs, while mammals are intermediate among life forms (Bateson, 1988; Gottlieb, pp. 95, 149), and the human genome demonstrably contains a

great deal of "junk DNA" (Pennisi, 2001). So other factors must be involved in evolution. Avital and Jablonka (2000) suggest that because behavioral plasticity can be so great, species can develop an underlying "large reservoir of genetic variation [that can be] exposed and recruited when the environment changes" (p. 323). Thus, if any genetically-supported capacity for environmental modification is present, it may be built upon without the necessity of major genome expansions (e.g., Gould's 1977 suggestion that changes in the timing of development were the basis for human evolution). Behavior change can lead to morphological change, for example, via a developmental process or simply the existing capacity for morphological flexibility (Wcislo, 1989; West-Eberhard, 1989; see Bernays, 1986, and Meyer, 1987, on diet-induced reversible morphological changes). Genetic change and speciation *can* also follow, although they *may* not.

Many examples are known or surmised for both operant and species-typical sources. "Upside down" flamingo feeding, an operant behavior that presumably developed through enhanced foraging opportunities, was followed by structural modification of the bird's bill (Gould, 1985, who includes several other examples; Wcislo, 1989). Behavior changes in bees, probably species-typical, led to nest parasitism, which was then followed by conditions that selected for genetic changes. Some structural changes that follow these behavioral changes can be developmentally induced in free-living (nonparasitic) individuals (Wcislo). Similar plasticity allows the reuse of maternal nests in bees without genetic changes, but this likely species-typical practice can, in turn, lead to different social structures, and eventual genome adjustment (West-Eberhard, 1989). Scrub jays in an isolated area speciated and developed markedly new social relations, perhaps a combination of species-typical and operant behaviors (Gray, 1988). Again, such changes can reasonably be due to any source, whether developmental changes affecting malleable species-typical behavior, or the inherent flexibility of operant learning and classical conditioning. Wilson (1992) suggested that Darwin's finches on the Galapagos developed tool-using accidentally. The technique was probably propagated

through observational learning, and birds with more flexible operant capabilities were more likely to succeed at it and pass on their genes. As Wilson summarized, "Evolutionary biologists believe that genetic assimilation of this kind can on occasion greatly accelerate evolution, with behavioral flexibility leading the way" (p. 103; see also Gottlieb, p. 150; Avital & Jablonka, 2000; Bateson, 1988; Gray, 1988; Wcislo; West-Eberhard). Behavioral flexibility can also retard genotypic evolution, however, since behavioral changes can remove the selective pressure for genetic changes (but see Avital & Jablonka, 2000).

The environment that supported such behavior/developmental changes can simply maintain them, as with the flamingos (for examples of other maintenance mechanisms, see Avital & Jablonka, 2000; Clark & Galef, 1988; Denenberg & Rosenberg, 1967; Ho, 1984, these three also cited in Gottlieb; Jablonka & Lamb, 1995; Suomi, 1999; Suomi & Levine, 1998). These changes can be as durable as genetic changes (Gray, 1988; Jablonka & Lamb). Further, direct behavioral mechanisms of transmission such as parental modeling and social learning are important and potentially long-lasting in nonhumans as well as humans (e.g., Avital & Jablonka). These mechanisms involve operant learning, of course.

Orcas, currently considered one species, may be in the midst of behaviorally-led speciation right now in the American Pacific Northwest: "Transient" orca pods are nomadic hunters largely of marine mammals, whereas "residents" remain in smaller territories and subsist mainly on fish (Hoelzel, Dahlheim, & Stern, 1998). Morphological differences between the two groups already exist (e.g., shape of dorsal fin), but these do not necessarily represent a change in the genome. The whales have not interbred for many generations, but could still do so. However, genetic change may eventually follow if the niches are sufficiently different and the subpopulations continue to be sufficiently reproductively isolated (see Irwin & Price, 1999). Only at this stage, according to current definition, has evolution occurred. Gottlieb considers that, given enough concurrent changes, "phenotypic evolution" can be considered to have occurred without any such ge-

netic change (see also Wcislo, 1989; West-Eberhard, 1989).

In ecological context, the nature of a niche interacts with behavioral plasticity (see Avital & Jablonka, 2000, for excellent examples). Strategists of the r and K types, for example, are the ends of a continuum, with some evolutionary pressures selecting rapid reproduction to take advantage of temporarily favorable conditions, producing populations that then fall back dramatically (r-type). Slow-reproducing K types are more stable, corresponding to their more stable environments. Gould (1977) found that correlated K-type effects include more brain development, more parental care, and greater longevity, all of which can lead to a greater likelihood of behavioral plasticity. Greater possibilities for sociality might ensue, with a role of recognition of individuals requiring discrimination learning (Fantino & Logan, 1979). Early enriched experiences may enhance the brain, as noted previously, and large-brained species may benefit more from these experiences (Gottlieb, p. 152). Species with larger brain mass/body mass ratios may exhibit faster rates of evolution, possibly due to a higher probability of behavioral neophenotypes (Gottlieb, pp. 155, 158, based on Jerison, 1973, and Wyles, Kunkel, & Wilson, 1983; Bateson, 1988; all also cited in Gottlieb; but see, e.g., Butler & Hodos, 1996, for critical commentary). These effects may also exist in some other species with complex social behaviors (Wcislo, 1989).

Alternatively, environments that remain very stable can foster a transition from learned behavior to the less flexible but faster-appearing species-typical behaviors (Avital & Jablonka, 2000). Learning researchers tend to assume that species-typical behaviors are an earlier-evolved, primitive form of behavior-environment relation, with operant capacities developing later either out of species-typical behaviors or the related ones of reflexes and tropisms. This may well have been the case, but the opposite direction is also possible. Most recently, Avital and Jablonka outlined how the transition from learned to non-learned response can occur, based on Waddington's classic fruit fly experiments and later work (e.g., Ewer, 1956, for imprinting). Phylogeny can recapitulate ontogeny!

Developmental and behavioral variables are critical in driving evolution, an idea that

traces back to Darwin himself and even earlier to Lamarck (Gould, 1985). Two of the earliest to produce detailed statements of the role of behavior in evolution were psychologists Lloyd Morgan and Baldwin (both 1896; see Wcislo, 1989, for current views). Despite this history, as Gottlieb points out, the idea has been neglected (also see Wcislo, 1989; West-Eberhard, 1989).

MECHANISMS AND INTERACTIONS

The interaction between genes, behavior, and environment on a more molecular level, fortunately, has been an active research area for years. The mechanisms behind Gottlieb's and other developmental induction phenomena are slowly being revealed (e.g., Parsons & Rogers, 2000, for imprinting). The importance of plasticity in Gottlieb's work and in evolutionary context already has been noted. The neuroscience revolution has revealed that the physiological systems supporting behavior may be as plastic as behavior itself, and the speed of response to environmental changes can be rapid, even in adulthood (Greenough & Sirevaag, 1991; Pascual-Leone & Hamilton, 2001). Gene expression is easily altered to produce morphological and physiological, as well as behavioral, changes (Avital & Jablonka, 2000). And, of course, the genome itself can be altered. Probabilistic epigenesis truly has considerable support.

Many everyday environmental events, such as winning a social contest, can affect hormone levels that affect gene expression over long periods (Wcislo, 1989). Sex changes occur in some fishes when the social hierarchy changes (Shapiro, 1980, also cited in Gottlieb). Behavioral as well as morphological changes are involved, and no sensitive period exists. Light can induce the setting of circadian rhythms in fruit flies (and other species) by changing gene expression (Gottlieb, p. 146). "Immediate early genes" can be activated quickly in response to external stimuli (e.g., Armstrong, & Montminy, 1993; Calamandrei & Keverne, 1994; Rosen, McCormack, Villa-Komaroff, & Mower, 1992, all as also cited in Gottlieb).

Reverse transcriptase (e.g., from the human immunodeficiency virus), certain chemicals (e.g., mutagens), and electromagnetic and ionizing radiation (e.g., ultraviolet and

radioactive emissions) are among the sources of actual DNA change. Portions of the human genome contain a number of genes from infectious bacteria (Pennisi, 2001). And interactions occur within the gene level, because within-cell self-copied genes and mobile genes can affect other genes; genomes must now be viewed as "fluid" (Gould, 1987; Ho, 1984, also cited in Gottlieb). All parts of the developmental genome-environment system are capable of influencing all the other parts (Gottlieb, p. 94; Ho, 1988; see Gottlieb, 1998, for additional examples).

EXPANDING HORIZONS

Nothing is "genetically determined" without environmental input. Scientists always knew that, but Gottlieb and others have shown just how significant the environmental input can be, even for "instinctive" behaviors. Gottlieb's probabilistic epigenesis describes the interaction of genes and environment at all levels, in all species, throughout the life cycle. Behavior principles are critical in these interactions. Although most learning researchers have long acknowledged these interactions, they have rarely explicitly investigated them. But where operants and respondents exist, learning researchers must follow.

The overarching principle for all life sciences is evolution, and behavior principles are likewise critical for understanding evolutionary processes. In turn, because of evolution, behavior principles exist, and it yet remains to be seen how well they can be reasonably categorized. The very definition of *learning* is rife with difficulty (Papaj & Prokopy, 1989). Evolution has produced many combinations of behavioral effects, such that we may even be dealing with continua rather than discrete entities. Yet, the evidence for general principles of learning is strong. Learning research will be the more valuable and useful if it takes into account what is known of the biology of behavior.

In addition, precedents suggest that a better understanding of the biological basis of behavioral phenomena may be required for learning research to be better integrated into scientific psychology and the applied realms (e.g., Field, 1993). The dismissal of learning research found even in the otherwise fine work of Pulitzer prize-winning authors like

Jonathan Weiner (1999; see also Todd & Morris, 1992) is a reason in itself to establish stronger connections with biology.

Other benefits of developmental and evolutionary work are just as substantial. The importance of behavioral history is well documented, and developmental processes *are* history. And evolutionary considerations can add an important perspective to behavioral analyses. More specifically, interdisciplinary studies of the provenance and nature of effective consequences are essential for operant analyses. The added sophistication and scope of the understanding of basic behavior-environment relations that will result can only carry over to applied work, with humans as well as nonhumans.

The substantive relevance of Gottlieb's and related work in psychobiology to the experimental analysis of behavior has long been recognized (e.g., Dougan, 1994; Fantino & Logan, 1979; Gottlieb, 1994; Midgley & Morris, 1992; Provine, 1988; Staddon, 1983; Verplanck, 1955). Both fields have significantly progressed since Schwartz's (1974) powerful review of Seligman and Hager's (1972) *Biological Boundaries of Learning*, but his goal of reconnecting the sciences of behavior still remains distant. Kuo (1976) himself was a lifelong self-proclaimed behaviorist who believed behaviorism's main tasks included obtaining "a comprehensive picture of the behavioral repertoire of the individual and its causal factors from stage to stage during development" (p. 26). If the experimental analysis of behavior is to contribute fully to the life sciences, its practitioners need to be aware of what they can learn from their co-disciplines, and what they can offer. Their expertise and knowledge base can enrich developmental psychobiology and evolutionary biology (as is sometimes recognized, e.g., Ho, 1988). In turn, their basic understanding and applications will benefit, as learning researchers affirm their place among the sciences subsumed by Darwin's grand scheme and contribute to the science of *all* behaviors. None of this abrogates traditional learning research, but puts it in larger context and provides valuable new resources. Can learning researchers be content without knowing how far their principles extend?

CONCLUSION

Psychology is part of biology. All behavior and brain processes are functions of the living organism, a biological substrate in interaction from conception with the environment. All behavioral capabilities, including species-typical behaviors and learning, are genetically influenced and physiologically supported. But the role of the environment is equally essential, critical in genetic expression as well as at higher levels. The nature-nurture false dichotomy, overturned so ably by Gottlieb among others, has been replaced by a fully interactional view. Biological and psychological efforts over the course of the 20th century have illuminated our understanding of how genes and environment jointly produce behavior within the larger evolutionary context. Gilbert Gottlieb's long-term research program exemplifies these accomplishments, and his book provides a valuable summary of both the research and the theory that have set the stage for biopsychology in the 21st century.

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