ECOLOGICAL PSYCHOLOGY, *12*(4), 319–334

An Ecological Approach to Behavioral Development: Insights From Comparative Psychology

Robert Lickliter
Department of Psychology
Virginia Polytechnic Institute and State University

In this article, I review recent work from comparative psychology, highlighting several conceptual and methodological insights drawn from comparative research and exploring their value to an ecological approach to behavioral development. In particular, I consider examples of a major focus of comparative psychology, the search for developmental mechanisms and processes underlying the expression of species-typical behavior. This focus has provided several insights regarding behavioral development that have supported an ecological approach and provided a richness and depth of perspective on behavior complementary to that found in ecological psychology. Specifically, I review the related notions of probabilism, equifinality, nonlinearity, and distributed control and discuss their applicability to and support of ecological theory.

Although the importance of context or milieu has been acknowledged in the behavioral sciences for many years (e.g, Brunswik, 1952; Kuo, 1967; Lewin, 1931; Schneirla, 1957; Werner, 1957), a concerted effort to include contextual factors in analytic studies of behavioral development is a relatively recent direction in psychological sciences (see Michel & Moore, 1995). This effort is part and parcel of the growing influence of an ecological approach to behavioral organization. As recently reviewed by Reed (1996), an ecological approach to behavior is a powerful addition to traditional psychological inquiry, in that it expands the scope of investigation and directs research attention beyond the boundary of the organism. In particular, an ecological approach views the relation between the organism and its environment, rather than the nature of the organism itself, as the appropriate object of study of psychology (J. J. Gibson, 1979/1986). This empirical concern with context

Requests for reprints should be sent to Robert Lickliter, Department of Psychology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061–0436. E-mail: duckling@vt.edu

or milieu is a major shift in research emphasis, as the science of psychology has tended to reduce the habitats or contexts of animals to "stimuli," making little attempt to examine the complex places and events within which normal behavioral development takes place (Reed, 1996). In contrast, an ecological approach views behavioral development as situated and stresses the fundamental connectedness of the organism to its surroundings. From this view, an organism's functional environment is structured, organized, and specific to the organism, and the task of defining the relevant features of an organism's context becomes an empirical problem that requires systematic description and analysis (Johnston, 1981, 1985).

Approaching behavioral development as a process that is situated highlights the need to specify in detail the variety of physical, biological, and social factors that the organism encounters as it develops over time. Of course, as an organism develops, its relation to the external world also changes, so that its effective environment changes as well (Johnston, 1985). One of the strengths of an ecological approach to behavioral development is its explicit attempt to elaborate an appropriately dynamic view of the changing relationship between the developing organism and its context. Indeed, one can argue that an ecological perspective provides a unique conceptual framework for investigating the changing organism in relationship to its changing physical, biological, and social environment (Reed, 1996; Tudge, Gray, & Hogan, 1997).

This attempt to adequately capture the dynamic and emergent nature of behavioral development is, of course, not unique to ecological psychology. Work from comparative psychology and developmental psychology also provide many useful examples of this challenging quest. Although insights and applications from developmental psychology are becoming increasingly well integrated into the ecological literature (i.e., Adolph, Eppler, & Gibson, 1993; Bahrick & Pickens, 1994; Dent-Read & Zukow-Goldring, 1997; Eppler, 1995; E. J. Gibson, 1969), contributions from comparative psychology remain relatively underrepresented (but see Burton, 1993; Johnston, 1981; Lickliter, 1991; Miller, 1997; Reed, 1982). Because the majority of ecological psychologists have little or no formal training in comparative psychology or animal behavior, they are not likely to be overly familiar with the theories, concepts, or methods employed by a comparative approach to the study of behavior. In this article, I briefly review recent work from comparative psychology, highlighting several conceptual and methodological insights from comparative research and their value to ecological psychology. In particular, I explore examples of a major focus of comparative psychology, the search for developmental mechanisms and processes underlying the expression of species-typical behavior. I argue that insights from this comparative approach to behavioral development have both supported the ecological view and have provided a richness and depth of perspective on behavior not often acknowledged by the ecological tradition. In particular, I explore notions of probabilism, equifinality, nonlinearity, and distributed control in terms of their applicability to and support of ecological theory.

THE PROBABILISTIC VIEW OF BEHAVIORAL DEVELOPMENT

One of the most important insights achieved by comparative psychology in this century is that behavior is not represented in a genetic or neurological template prior to its emergence. This hard-won insight of *probabilistic epigenesis* (see Gottlieb, 1992, 1997, for historical overviews) replaced the notion of predeterminism, in which behavioral development was seen to progress in an orderly and preordained sequence under the control of genetic or neural substrates (Ausubel, 1957; Gottlieb, 1970). From this view, genes are seen to be deterministic, guiding the nervous system to mature in a predetermined fashion, giving rise to innate or instinctive behavior. Thanks in large part to more than a half of century of comparative–developmental research (e.g., Gottlieb, 1971; Kuo, 1967; Lehrman, 1970; Schneirla, 1966), most psychologists now appreciate that behavior does not unfold from some predetermined template or blueprint. Behavior is increasingly viewed as a system property, a result of transactions between the organism and its environment over the course of individual ontogeny. From this view, *species-typical behavior* is a descriptive term that denotes a range of behavioral functions that develop under conditions and situations typical of a particular species (Schneirla, 1966) and does not connote innate or predetermined patterns of behavior. Conventional assumptions of innate or hard-wired behavior (see Eibl-Eibesfeldt, 1989; Mayr, 1974) have gradually given way to the realization that genes cannot, in and of themselves, produce behavioral traits or characteristics (Gottlieb, Wahlsten, & Lickliter, 1998). Rather, at the level of behavior, the organism and its surroundings constitute an integrated system, and genetic, neural, or physiological factors are always part of the organism's entire developmental system, including contextual factors extrinsic to the organism (for more detailed discussions, see Gottlieb, 1991; Oyama, 1985).

This coactional, hierarchical systems view and its focus on the reciprocal interactions among constituent parts and levels highlights the fact that behavioral development is an emergent phenomenon regulated jointly by organismic and contextual factors. In this view of development, the various and varied changes, improvements, and reorganizations in an organism's behavior do not represent the unfolding of a fixed or predetermined substrate, independent of the activity, experience, or setting of the organism. Much of the empirical support for this epigenetic–systems view of behavior has come from comparative research (for multiple examples, see Michel & Moore, 1995), due in part to the inherent limitations associated with human research. Because animal studies allow experiential modification techniques such as enhancement, deprivation, or transposition during both prenatal and postnatal periods, they permit detailed and systematic investigation of the specific organismic and environmental conditions necessary for normal or species-typical behavior to occur. This type of work has yielded several key insights into the probabilistic nature of behavioral development, which are beginning to be incorporated into related disciplines outside comparative–developmental psychology (see Shanahan, Valsiner, & Gottlieb, 1997). One of the most important of these is the notion of equifinality.

EQUIFINALITY

The predeterministic assumption that behavioral development follows a relatively immutable sequence that arrives at a predisposed endpoint has been repeatedly challenged by the empirical demonstration of *equifinality,* in which the same ability or capacity may arise from quite different developmental pathways and processes. The notion of equifinality was originally proposed in embryology (Driesch, 1929) and has been demonstrated experimentally in a number of recent comparative behavioral studies (Banker & Lickliter, 1993; Gottlieb, 1997; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Miller, Hicinbothom, & Blaich, 1990). The results of these studies all highlight the emergent nature of behavioral development and provide converging evidence that there are potentially multiple developmental pathways or trajectories to normal or species-typical outcomes. The results of these studies argue against a deterministic view of behavior, one in which there is little variability in the developmental pathway leading to a particular endpoint or outcome.

As a case in point, Banker and Lickliter (1993) explored the relative impact of early versus delayed visual experience on intersensory development by manipulating the timing of visual experience of bobwhite quail embryos and chicks during the perinatal period. In particular, a limitation of sensory experience that is normally present in early development (absence of patterned visual experience prenatally) was removed by opening the egg and providing the embryos patterned visual stimulation, and a limitation of sensory experience that is not normally present in early development (no patterned visual experience postnatally) was provided the same subjects by rearing them from hatching with eye patches. Under normal rearing conditions, concurrent information from the visual and auditory systems is not present prenatally but is typically present following hatching. Experimentally reversing this pattern of intersensory experience resulted in the same species-typical pattern of perceptual responsiveness to maternal auditory and visual information seen in normally reared, unmanipulated chicks. In contrast, chicks that received either enhanced patterned visual experience prenatally or attenuated visual experience postnatally showed altered patterns of species-typical perceptual responsiveness to maternal information. The finding that quail chicks receiving both early visual experience as embryos and delayed visual experience as hatchlings exhibited a pattern of auditory and visual responsiveness like that seen in normally reared chicks illustrates the possibility of variation in developmental pathways to species-typical behavioral outcomes and punctuates the inadequacy of predeterministic frameworks in capturing the emergent and malleable nature of behavioral development.

A study by Lickliter and Hellewell (1992) also served to make this point. In this study, bobwhite quail embryos were found to be capable of learning an individual bobwhite maternal call during the prenatal period (before hatching), whereas bobwhite hatchlings did not demonstrate the ability to learn an individual maternal call after hatching. However, when embryos were provided prenatal visual experience while being exposed to the maternal call, they did not learn the maternal call (thus appearing like normally reared hatchlings). Likewise, when hatchlings were reared under conditions of reduced visual experience during exposure to the call, they did successfully learn the individual maternal call (thus appearing like normally reared embryos). These results provide further evidence that the same behavioral outcome can be achieved by markedly different developmental means or pathways (for a similar prenatal example, see Lickliter & Lewkowicz, 1995). Miller et al. (1990) likewise showed how different developmental events (in this case, prenatal auditory experience or postnatal social experience) can lead to the same species-typical behavior (freezing response to the maternal alarm call) in ducklings.

Taken together, these various comparative studies show that (a) developing organisms that have different early conditions can reach the same behavioral endpoint and (b) organisms can reach the same endpoint by different routes or pathways. As recently noted by Gottlieb (1997), this principle of equifinality is potentially one of the most important insights of contemporary developmental theory for understanding both normal and abnormal behavior, as it suggests that there is more than one developmental route to normal behavioral or psychological organization and more than one route to any particular behavioral or psychological disorder. Such a view has far-reaching implications for both the diagnosis and treatment of various behavioral or psychological problems.

NONLINEARITY

Besides highlighting the dynamic and emergent nature of behavioral development, comparative studies also serve to demonstrate the concept of *nonlinearity.* This notion, that developmental outcomes may not be predictable in any simple, linear causal way, is often represented by the term *nonobvious,* in that experiential influences that maintain, facilitate, or induce a particular behavioral outcome are often markedly dissimilar from that outcome (Gottlieb, 1991; Miller, 1997). In other words, behavior may be dramatically influenced by aspects of the organism's exposure or experience with events and relations that share neither time nor function in common with the behavior of interest. Research from comparative psychology has repeatedly demonstrated that investigators must often consider the developmental consequences of an organism's varied encounters with its environment that have no intuitive or straightforward relation to the behavior pattern under study (e.g., West & King, 1996; Miller, 1997). For example, a number of studies have found that perinatal auditory experience can affect subsequent visual responsiveness in avian hatchlings (Dyer & Gottlieb, 1990; Lickliter & Stoumbos, 1991; McBride & Lickliter, 1994; Sleigh & Lickliter, 1997) and that social experience with conspecifics can significantly affect chicks' auditory or visual discrimination abilities in the days following hatching (Columbus & Lickliter, 1998; Gottlieb, 1993; Lickliter & Gottlieb, 1985; McBride & Lickliter, 1993; Miller, 1994).

Along with equifinality, the phenomenon of nonlinearity stresses the importance of not side-stepping the task of *developmental analysis,* that is, of empirically identifying the various features of an organism's developmental system that are necessary to produce normal, species-typical behavior. Importantly, developmental analysis requires recognition that the organism and its environment are functionally reciprocating components of a unified system, a view articulated by several noted comparative psychologists nearly 50 years ago (Lehrman, 1953; Schneirla, 1957; Werner, 1957). A compelling contemporary example of such developmental analysis comes from Gilbert Gottlieb's 3 decades of investigation of the process of species identification in precocial birds (reviewed in Gottlieb, 1971, 1997). This body of work provided numerous examples of the nonobvious (nonlinear) nature of the development of so-called instinctive behavior.

To briefly summarize a pertinent example, Gottlieb (1980) found that duck embryos that have been denied normally occurring exposure to their own and sibling-produced vocalizations during the late prenatal period subsequently fail to show a species-typical preference for their species' maternal assembly call. In other words, to exhibit normal, species-typical responsiveness to their hen's maternal vocalizations, young ducklings must hear either their own or their siblings embryonic vocalizations during early development. Birds denied this opportunity fail to show species-specific preferences in the period following hatching. The intricacy of the developmental causal network revealed in this work was remarkable. For example, Gottlieb found that not only must the duckling experience the vocalizations as an embryo, the embryo must experience *embryonic* vocalizations (after hatching, such experience was found to be ineffective). This demonstration of the link between ducklings' exposure to their own vocalizations and their subsequent responsiveness to their maternal hen's species-specific call typifies the nonlinear nature of behavioral development discussed previously, in that a seemingly subtle feature of experience turned out to have a significant effect on a particular (but dissimilar) developmental outcome.

Recently, Miller (1997) proposed that there is often an inverse relation between the obviousness of experience and the extent of the species typicality of behavior. In other words, the greater the stereotypy of the behavioral outcome, the less obvious are the experiences that influence or foster its development. For example, Wallman (1979) found that preventing young chicks from seeing their own feet in the days following hatching affects their feeding responses to mealworms. When chicks were not permitted to see their toes during the first 2 days after hatching, they did not eat or even pick up mealworms, a stereotyped response reliably seen in normally reared chicks. Cramer, Pfister, and Haig (1988) found that the normal preweaning experience of nipple shifting during suckling bouts significantly influenced rat pups' later success in solving a spatial learning (radial-arm maze) problem. The early experience of nipple shifting apparently contributed to adopting a "win-shift" strategy essential to solving the spatial maze problem. Whether or not Miller's proposal of an inverse relation between the nature of nonobvious experience and species typicality holds up under more systematic examination, the phenomenon of nonlinearity nonetheless highlights the need (and dividends) of expanding our awareness of the possible significance of nonobvious forms of experience on the achievement of specific behavioral skills or abilities. Investigators must not assume that they need to manipulate only the most obvious forms of context or experience to identify causal variables. Rather, an organism's environments must be reported and analyzed in greater detail and multiple assessments of the developmental resources they provide may be required over the course of ontogeny (Ronca & Alberts, 1995; Smotherman & Robinson, 1995). Logical intuition for what constitutes important influences on outcomes may work well at times for simple systems but can often impede our understanding of complex, multidetermined phenomena like the emergence and subsequent organization of behavior.

DISTRIBUTED CONTROL

The concepts of equifinality and nonlinearity complement the relatively recent realization that the consequences of change in one component of a complex developmental system often depends on the preceding, current, or succeeding state of other components in that system (for discussions, see Cohen & Stewart, 1994; Thelen & Smith, 1994). From this view, behavior is always the complex product of many interacting factors, and it is misleading to attribute primary causal status to any one factor acting in isolation. This important idea of *distributed control,* that control for any behavioral outcome resides in the nature of the relation within and between organismic and contextual variables, is still not widely appreciated in much of psychology. Unidirectional, additive causal thinking continues to pervade much of our discipline (for recent critiques, see Shanahan et al., 1997; Valsiner, 1987). However, investigators working in a number of areas (particularly comparative and developmental psychology) are becoming increasingly sensitive to the fact that the functional significance of genes, neural structures, hormonal levels, or any external influence on behavior can be understood only in relation to the larger developmental system of which they are a part. At each level of the system, the effect of any source of influence is potentially dependent on the rest of the system, making all factors inherently interdependent and mutually constraining (Gottlieb, 1991, 1997; Oyama, 1985, 1993).

Results from comparative work provide growing evidence for the insight that control for any behavioral outcome resides in the dynamic nature of relations between intraorganismic and extraorganismic factors. For example, results from the study of the development of intersensory perception demonstrate that nonspecific sensory information such as intensity or amount of stimulation can interact with specific organismic characteristics such as the state of arousal of the infant and the context of the infant to contribute to the infant's emerging capacity for specific intersensory functions. For example, as their own arousal levels increase, infants typically decrease their responsiveness to higher levels of external stimulation; when arousal levels are lowered, responsiveness to higher levels of external stimulation is observed (Lickliter & Lewkowicz, 1995; Sleigh & Lickliter, 1997; for examples from human development, see Gardner & Karmel, 1995; Lewkowicz & Turkewitz, 1981). Analysis at both the neural and behavioral level has revealed individual intersensory functioning to be multidetermined, with diverse internal and external variables interacting, often in a nonlinear fashion. For example, how prenatal sensory stimulation influences early perceptual development appears to depend on a number of nested factors, including the timing of the sensory stimulation relative to the developmental stage of the organism, the type of sensory stimulation provided, as well as the amount of sensory stimulation provided or denied. These factors and their influence seem to interact and to change with the organism's context, state, and developmental history (Lickliter, 1985; Sleigh & Lickliter, 1997; Turkewitz, 1994; Turkewitz & Mellon, 1989).

A key factor associated with the influence of prenatal sensory experience on early perceptual development is the overall amount of stimulation the developing organism encounters. Based on their findings from enhanced vestibular stimulation in duck embryos, Radell and Gottlieb (1992) recently hypothesized that the typical developmental context of an organism provides an optimal amount of stimulation for species-typical perceptual development. In other words, sensory experience that falls within a range of stimulation typical for a particular species should not interfere with intersensory development, but stimulation that exceeds or falls short of that optimal range should potentially cause functional deficits in normal patterns of perceptual functioning. Subsequent experiments have lent support to the existence of some optimal range of perinatal sensory experience necessary for normal development (Carlsen & Lickliter, 1999; Lickliter & Lewkowicz, 1995; Sleigh & Lickliter, 1996, 1997). For example, Radell and Gottlieb demonstrated that mallard duckling embryos fail to learn an individual mallard maternal call when exposed concurrently to enhanced vestibular stimulation but do demonstrate auditory learning ability when the amount of vestibular stimulation is reduced to more closely approximate their normal range of prenatal vestibular experience. In keeping with the notion of distributed control and reciprocal interaction, related work with quail embryos has shown that the type of prenatal sensory stimulation the organism encounters can also be an important influence on subsequent perceptual functioning, often mediating what constitutes an optimal amount of stimulation needed to maintain or facilitate species-typical development. That is, the amount of stimulation that falls within the optimal range appears to change depending on the particular type of sensory stimulation that is being encountered by the developing organism. For example, quail embryos show enhanced perceptual functioning when exposed to slightly increased amounts of their own contentment calls prior to hatching but delayed perceptual development when exposed to their own distress calls during the prenatal period. These patterns of responsiveness depend not only on the type of auditory stimulation provided but also on the amount of auditory stimulation present in the prenatal environment. Embryos exposed to greatly increased amounts of contentment calls showed delayed perceptual development and decreased survivability (Sleigh & Lickliter, 1996, 1997). Similar results have also been reported for increased amounts of prenatal tactile and vestibular stimulation (Carlsen & Lickliter, 1999).

Of course, under normally occurring conditions, the structured and sequestered environment provided by the avian egg serves to reduce the possible degrees of freedom contributing to the chick's early perceptual organization (Lickliter, 1995). This *constraints by design* notion provides possible insight into how stable and reliable perceptual outcomes within a species are achieved during early development. Specifically, limits in the amount and type of sensory stimulation experienced during prenatal development as a result of the buffered, protected nature of the egg (or the uterine environment of mammals) seems to provide an orderly structure for the developing embryo or fetus and significantly influences the nature of intersensory relations during the perinatal period (Turkewitz & Kenny, 1982). In this view, both the limited sensory capacities of the prenatal organism and the buffered prenatal developmental context combine to provide constraints that minimize the simultaneous or concurrent presentation of multiple sources of information to the developing embryo or fetus. The notion of an orderly context for development is consistent with an ecological view of development that recognizes that the organism–environment relation is one that is structured on both sides. Work from comparative psychology extends this view by demonstrating that the epigenetic emergence of early behavioral capacities is both guided and constrained by features of the organism as well as by features of its developmental context.

INTEGRATION OF COMPARATIVE INSIGHTS ON BEHAVIORAL DEVELOPMENT: SOCIAL EXPERIENCE AND PERCEPTUAL DEVELOPMENT

An arena of comparative research that brings together the various insights about behavior reviewed in this article (probabilism, equifinality, nonlinearity, and distributed control) is the role of social experience in the development of perceptual, social, and cognitive processes in a variety of animal species (e.g., Blaich & Miller, 1986; Hofer, 1987; Khayutin, 1985; Lickliter, 1991; Mason, 1978; Miller, 1994;

Porter, Cernoch, & Matachik, 1983; Wang & Novak, 1992). Most developing avian and mammalian infants are typically embedded within a rich social network of conspecifics. In addition to providing nurturance and protection to the developing organism, the social environment provides varied and complex patterns of experience, including thermal, tactile, olfactory, auditory, and visual stimulation. This species-typical social stimulation, present prenatally for many species and postnatally for most species, is increasingly recognized as an important component of normal experience that can actively influence behavioral development. Conspecifics can be viewed as experiential resources to the developing organism and have been found to play a significant role in the development and maintenance of species-typical behavior (Lickliter, Dyer, & McBride, 1993; West & King, 1987, 1996).

For example, work with precocial birds has repeatedly demonstrated that the particular types and amounts of sensory stimulation provided by the hatchling's immediate social environment can dramatically influence the young bird's perceptual and social preferences during prenatal (Gottlieb, 1980; Lickliter & Lewkowicz, 1995) and postnatal periods (Gottlieb, 1993; Lickliter & Gottlieb, 1985; Miller, 1994). In most cases, these influences are nonobvious, in that observed behaviors in response to maternal information (one type of interaction) are often influenced and supported by early experience with siblings (a different type of interaction). In this light, recent research with bobwhite quail has provided converging evidence that physical interaction with siblings can significantly influence young chicks' perceptual responsiveness to both maternal auditory and visual information following hatching. Chicks who were reared in relative social isolation during the prenatal (Sleigh, Columbus, & Lickliter, 1996; Sleigh & Lickliter, 1996) or postnatal periods (McBride & Lickliter, 1993) or who were reared with quail chicks of another species (McBride & Lickliter, 1993) failed to prefer species-specific maternal auditory and visual information at ages, when unmanipulated, socially reared chicks reliably demonstrated such social preferences. The specific features of chicks' social interaction with their broodmates necessary to maintain the emergence of normal patterns of intersensory responsiveness are currently poorly understood (but see Columbus & Lickliter, 1998; Gottlieb, 1993), but it is clear that increased experimental attention to naturally occurring social factors is an important addition to the analysis of species-typical behavioral development.

In the general sense, these studies concerned with the social factors underlying normal behavioral development in precocial birds illustrate the (a) malleability of early intersensory functioning, (b) the nonlinear and distributed nature of the factors contributing to the emergence of species-typical behavior, and (c) the indeterministic nature of behavioral development. In all cases, specific developmental outcomes were often not predictable in any simple, linear way from their antecedents (for examples drawn from work with altricial birds, see West & King, 1996).

The underappreciation of these related principles in much of psychology perpetuates a reductionistic view of the underlying causes of behavior. Namely, many psychologists continue to take for granted that behavior is somehow determined by more fundamental or primary processes that occur at the genetic or neurophysiological level (e.g., Gazzaniga, 1992; Tooby & Cosmides, 1990). This linear, unidirectional, bottom-up view of the causes of behavior overlooks the fact that genetic or neural factors are always part and parcel of the individual organism's entire developmental system. No single element or level in the system necessarily has causal primacy or privilege, and the functional significance of genes, neural structures, or any other influence on behavior development can be understood only in relation to the developmental system of which they are a part. The minimum unit for developmental analysis must be the developmental system, comprised of both the organism and the specific set of physical, biological, and social factors with which it interacts over ontogeny (Gottlieb, 1997; Kuo, 1967; Oyama, 1985).

A LOOK TOWARDS AN INTEGRATIVE PSYCHOLOGY

The conceptual and methodological insights reviewed in this article lead to a somewhat unconventional view of heredity, one that recognizes that what is inherited in reproduction are genes and the developmentally relevant features of the organism's species-typical environment. In other words, it is developmental systems, including not only the genes but also the features of the environment that support and influence development, that are transmitted between generations (Johnston & Gottlieb, 1990; Oyama, 1985). By characterizing not only the genes but also the stimulative developmental context as partners in providing the necessary elements for behavioral development, this expanded view of heredity makes the organism–context transaction process the explicit object of study, thereby including a large class of extragenetic variables that have often been omitted from explanations of species-typical behavior.

Of course, ecological psychology has long appreciated and promoted the view that the relation between the organism and its environment, rather than the organism itself, is the appropriate object of study for psychology (Reed, 1996). J. J. Gibson (1966) argued for an approach to the study of perception in which the researcher is explicitly concerned with the structure of the environment, of how the organism moves about in it, and of what sorts of perceptual information the environment provides the perceiving organism. From this approach, perception depends on the kinds of experiences that come from having a body with various sensory and motor capacities that are themselves embedded in a more encompassing physical, biological, psychological, and social context (see also Varela, Thompson, & Rosch, 1991).

Theory and research drawn from comparative psychology serves to amplify and extend this view, acknowledging and providing evidence that there is no top-down or bottom-up explanation of behavior that can be both necessary and sufficient. This perspective explicitly recognizes that a strict emphasis on any single domain or level in the developmental system, be it genes, physiology, neuroanatomy or neurochemistry, social interactions, or culture, will be too limited to successfully address the development and maintenance of behavior. Because behavioral development always depends on coactions involving the organism and its context, the task of defining the relevant developmental resources of an organism's internal and external milieu becomes the foundation of any systematic description or analysis of behavior. Students of behavior must be prepared to acquire precise and detailed information about the experiential stimulation present during the course of the individual organism's development if they are to successfully design experiments to understand that development. This focus serves to broaden and redefine the traditional scope of psychological inquiry and, in so doing, directs research attention to the important but often overlooked question of how behavioral possibilities and capacities emerge in process. The organism does not come into the world with ready-made response systems; rather, these systems emerge through dynamic transactions occurring across levels of organization comprising the organism–environment system. One of the primary tasks of the psychological sciences is to gain a deeper and more comprehensive insight into this complex, multidetermined process, and comparative psychology has and will continue to provide important conceptual and methodological tools for this challenging quest.

ACKNOWLEDGMENTS

The writing of this article was supported by National Institute of Mental Health Grants RO1–MH48949 and KO2–MH01210.

I thank Lorraine Bahrick and David Lewkowicz for their constructive comments.

REFERENCES

Adolph, K. E., Eppler, M. A., & Gibson, E. J. (1993). Development of perception of affordances. In C. Rovee-Collier & L. P. Lipsett (Eds.), *Advances in infancy research* (Vol. 8, pp. 52–98). Norwood, NJ: Ablex.

Ausubel, D. (1957). *Theory and problems of child development.* New York: Grune & Stratton.

Bahrick, L. E., & Pickens, J. (1994). Amodal relations: The basis for intermodal perception and learning in infancy. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception* (pp. 205–233). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Banker, H., & Lickliter, R. (1993). Effects of early or delayed visual experience on perceptual development in bobwhite quail chicks. *Developmental Psychobiology, 26,* 155–170.

Blaich, C. F., & Miller, D. B. (1986). Alarm call responsivity of mallard ducklings: IV. Effects of social experience. *Journal of Comparative Psychology, 100,* 401–405.

Brunswik, E. (1952). *The conceptual framework of psychology.* Chicago: University of Chicago Press.

Burton, G. (1993). Behavioral relics and animal–environment mutualism: Commentary on Coss. *Ecological Psychology, 5,* 153–169.
Carlsen, R., & Lickliter, R. (1999). Augmented prenatal tactile and vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychobiology, 35,* 215–225.
Cohen, J., & Stewart, I. (1994). *The collapse of chaos.* New York: Penguin.
Columbus, R. F., & Lickliter, R. (1998). Modified sensory features of social stimulation alters the perceptual responsiveness of bobwhite quail chicks. *Journal of Comparative Psychology, 112,* 161–169.
Cramer, C. P., Pfister, J. P., & Haig, K. A. (1988). Experience during suckling alters later spatial learning. *Developmental Psychobiology, 21,* 1–24.
Dent-Read, C., & Zukow-Goldring, P. (1997). *Evolving explanations of development: Ecological approaches to organism–environment systems.* Washington, DC: American Psychological Association.
Driesch, H. (1929). *The science and philosophy of the organism.* London: Black.
Dyer, A. B., & Gottlieb, G. (1990). Auditory basis of maternal attachment in ducklings under simulated naturalistic imprinting conditions. *Journal of Comparative Psychology, 104,* 190–194.
Eibl-Eibesfeldt, I. (1989). *Human ethology.* New York: de Gruyter.
Eppler, M. A. (1995). Development of manipulatory skills and the deployment of attention. *Infant Behavior and Development, 18,* 391–405.
Gardner, J., & Karmel, B. (1995). Development of arousal-modulated visual preferences in early infancy. *Developmental Psychology, 31,* 473–482.
Gazzaniga, M. S. (1992). *Nature's mind.* New York: Basic Books
Gibson, E. J. (1969). *Principles of perceptual learning and development.* Englewood Cliffs, NJ: Prentice Hall.
Gibson, J. J. (1966). *The senses considered as perceptual systems.* Boston: Houghton-Mifflin.
Gibson, J. J. (1986). *The ecological approach to visual perception.* Hillsdale, NJ: Lawrence Erlbaum Associates, Inc. (Original work published 1979)
Gottlieb, G. (1970). Conceptions of prenatal behavior. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 111–137). San Francisco: Freeman.
Gottlieb, G. (1971). *Development of species identification in birds: An inquiry into the prenatal determinants of perception.* Chicago: University of Chicago Press.
Gottlieb, G. (1980). Development of species-identification in ducklings: VI. Specific embryonic experience required to maintain species-typical perception in Peking ducklings. *Journal of Comparative and Physiological Psychology, 94,* 579–587.
Gottlieb, G. (1991). Experiential canalization of behavioral development: Theory. *Developmental Psychology, 27,* 4–13.
Gottlieb, G. (1992). *Individual development and evolution: The genesis of novel behavior.* New York: Oxford University Press.
Gottlieb, G. (1993). Social induction of malleability in ducklings: Sensory basis and psychological mechanism. *Animal Behaviour, 45,* 707–719.
Gottlieb, G. (1997). *Synthesizing nature–nurture: Prenatal roots of instinctive behavior.* Mahwah, NJ: Lawrence Erlbaum Associates, Inc.
Gottlieb, G., Wahlsten, D., & Lickliter, R. (1998). The significance of biology for human development: A developmental psychobiological systems view. In R. Lerner (Ed.), *Handbook of child psychology: Theory* (Vol. 1, pp. 233–273). New York: Wiley.
Hofer, M. A. (1987). Early social relationships: A psychobiologist's view. *Child Development, 58,* 633–647.
Johnston, T. D. (1981). Contrasting approaches to a theory of learning. *Behavioral and Brain Sciences, 4,* 125–173.
Johnston, T. D. (1985). Environmental constraints and the natural context of behavior: Grounds for an ecological approach to the study of infant perception. In G. Gottlieb & N. A. Krasnegor (Eds.), *Measurement of audition and vision in the first year of postnatal life* (pp. 91–108). Norwood, NJ: Ablex.

Johnston, T. D., & Gottlieb, G. (1990). Neophenogenesis: A developmental theory of phenotypic evolution. *Journal of Theoretical Biology, 147,* 471–495.
Khayutin, S. N. (1985). Sensory factors in the behavioral ontogeny of altricial birds. *Advances in the Study of Behavior, 15,* 105–134.
Kuo, Z. -Y. (1967). *The dynamics of behavior development.* New York: Random House.
Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology, 28,* 337–363.
Lehrman, D. S. (1970). Semantic and conceptual issues in the nature–nurture problem. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 17–52). San Francisco: Freeman.
Lewin, K. (1931). Environmental forces in child behavior and development. In C. Murchison (Ed.), *A handbook of child psychology* (pp. 94–127). Worcester, MA: Clark University Press.
Lewkowicz, D. J., & Turkewitz, G. (1981). Intersensory interaction in newborns: Modification of visual preferences following exposure to sound. *Child Development, 52,* 827–832.
Lickliter, R. (1991). Animal behavior and context: II. The role of conspecifics in species-typical perceptual preferences. *Ecological Psychology, 3,* 11–23.
Lickliter, R. (1995). Embryonic sensory experience and intersensory development in precocial birds. In J. P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychobiological perspective* (pp. 281–294). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
Lickliter, R., Dyer, A. B., & McBride, T. (1993). Perceptual consequences of early social experience in precocial birds. *Behavioural Processes, 30,* 185–200.
Lickliter, R., & Gottlieb, G. (1985). Social interaction with siblings is necessary for the visual imprinting of species-specific maternal preference in ducklings. *Journal of Comparative Psychology, 99,* 371–378.
Lickliter, R., & Hellewell, T. B. (1992). Contextual determinants of auditory learning in bobwhite quail embryos and hatchlings. *Developmental Psychobiology, 25,* 17–24.
Lickliter, R., & Lewkowicz, D. J. (1995). Intersensory experience and early perceptual development: Attenuated prenatal sensory stimulation affects postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychology, 31,* 609–618.
Lickliter, R., & Stoumbos, J. (1991). Enhanced prenatal auditory experience facilitates postnatal visual responsiveness in bobwhite quail chicks. *Journal of Comparative Psychology, 105,* 89–94.
Mason, W. A. (1978). Social experience and primate cognitive development. In G. M. Burghardt & M. Bekoff (Eds.), *The development of behavior: Comparative and evolutionary aspects* (pp. 233–251). New York: Garland.
Mayr, E. (1974). Behavior programs and evolutionary strategies. *American Scientist, 63,* 650–659.
McBride, T., & Lickliter, R. (1993). Social experience with siblings fosters species-specific responsiveness to maternal cues in bobwhite quail chicks. *Journal of Comparative Psychology, 107,* 320–327.
McBride, T., & Lickliter, R. (1994). Specific postnatal auditory stimulation interferes with species-typical visual responsiveness in bobwhite quail chicks. *Developmental Psychobiology, 27,* 169–183.
Michel, G. F., & Moore, C. L. (1995). *Developmental psychobiology: An interdisciplinary science.* Cambridge, MA: MIT Press.
Miller, D. B. (1994). Social context affects the ontogeny of instinctive behaviour. *Animal Behaviour, 48,* 627–634.
Miller, D. B. (1997). The effects of nonobvious forms of experience on the development of instinctive behavior. In C. Dent-Reed & P. Zukow-Goldring (Eds.), *Evolving explanations of development* (pp. 457–507). Washington, DC: American Psychological Association.
Miller, D. B., Hicinbothom, G., & Blaich, C. F. (1990). Alarm call responsivity of mallard ducklings: Multiple pathways in behavioural development. *Animal Behaviour, 39,* 1207–1212.
Oyama, S. (1985). *The ontogeny of information: Developmental systems and evolution.* New York: Cambridge University Press.
Oyama, S. (1993). Constraints and development. *Netherlands Journal of Zoology, 43,* 6–16.

Porter, R. H., Cernoch, J. M., & Matochik, J. A. (1983). Littermate influences on behavioral development in *Acomys cabirinus* and *Mus musculus. Zeitschrift Tierpsychologie, 62,* 93–104.

Radell, P. L., & Gottlieb, G. (1992). Developmental intersensory interference: Augmented prenatal sensory experience interferes with auditory learning in duck embryos. *Developmental Psychology, 28,* 795–803.

Reed, E. S. (1982). Darwin's worms: A case-study in evolutionary psychology. *Behaviorism, 10,* 165–185.

Reed, E. S. (1996). *Encountering the world: Towards an ecological psychology.* New York: Oxford University Press.

Ronca, A. E., & Alberts, J. R. (1995). Maternal contributions to fetal experience and the transition from prenatal to postnatal life. In J. P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychobiological perspective* (pp. 331–350). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Schneirla, T. C. (1957). The concept of development in comparative psychology. In D. B. Harris (Ed.), *The concept of development* (pp.78–108). Minneapolis: University of Minnesota Press.

Schneirla, T. C. (1966). Behavioral development and comparative psychology. *Quarterly Review of Biology, 41,* 283–302.

Shanahan, M. J., Valsiner, J., & Gottlieb, G. (1997). Developmental concepts across disciplines. In J. Tudge, M. J. Shanahan, & J. Valsiner (Eds.), *Comparisons in human development* (pp. 34–71). Cambridge, England: Cambridge University Press.

Sleigh, M. J., Columbus, R. F., & Lickliter, R. (1996). Type of prenatal sensory experience affects prenatal auditory learning in bobwhite quail. *Journal of Comparative Psychology, 110,* 233–242.

Sleigh, M. J., & Lickliter, R. (1996). Type and amount of prenatal stimulation alters perceptual responsiveness in bobwhite quail chicks. *Infant Behavior and Development, 19,* 325–338.

Sleigh, M. J., & Lickliter, R. (1997). Augmented prenatal auditory stimulation alters postnatal perception, arousal, and survival in bobwhite quail chicks. *Developmental Psychobiology, 30,* 201–212.

Smotherman, W. P., & Robinson, S. R. (1995). Tracing developmental trajectories into the prenatal period. In J. P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychobiological perspective* (pp. 15–32). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Thelen, E., & Smith, L. B. (1994). *A dynamic systems approach to the development of cognition and action.* Cambridge, MA: MIT Press.

Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology, 11,* 375–424.

Tudge, J., Gray, J. T., & Hogan, D. M. (1997). Ecological perspectives in human development: A comparison of Gibson and Bronfenbrenner. In J. Tudge, M. J. Shanahan, & J. Valsiner (Eds.), *Comparisons in human development* (pp. 72–105). Cambridge, England: Cambridge University Press.

Turkewitz, G. (1994). Sources of order for intersensory functioning. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception* (pp. 3–17). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Turkewitz, G., & Kenny, P.A. (1982). Limitations on input as a basis for neural organization and perceptual development: A preliminary theoretical statement. *Developmental Psychobiology, 15,* 357–368.

Turkewitz, G., & Mellon, R. C. (1989). Dynamic organization of intersensory function. *Canadian Journal of Psychology, 43,* 286–301.

Valsiner, J. (1987). *Culture and the development of children's action.* New York: Wiley.

Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied mind: Cognitive science and human experience.* Cambridge, MA: MIT Press.

Wallman, J. (1979). A minimal visual restriction experiment: Preventing chicks from seeing their feet affects later responses to mealworms. *Developmental Psychobiology, 12,* 391–397.

Wang, A., & Novak, M. (1992). Influence of social environment on parental behavior and pup development in meadow voles and prairie voles. *Journal of Comparative Psychology, 106,* 163–171.

Werner, H. (1957). The concept of development from a comparative and organismic point of view. In D. B. Harris (Ed.), *The concept of development* (pp. 125–48). Minneapolis: University of Minnesota Press.

West, M. J., & King, A. P. (1987). Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology, 20,* 549–562.

West, M. J. & King, A. P. (1996). Eco-gen-actics: A systems approach to the ontogeny of avian communication. In D. E. Kroodsma & E. H. Miller (Eds.), *The evolution and ecology of acoustic communication in birds* (pp. 20–38). Ithaca, NY: Cornell University Press.