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Comparative Psychology, A New Perspective for the 21st Century: Up the Spiral Staircase

ABSTRACT: *This article responds to the continuing obituaries for Comparative Psychology. We understand the field to be a general psychology, a way of understanding the origins of all behavior of all species. We outline a methodological and conceptual foundation for comparative psychology to enter the new millennium—with an anagenetic and dynamic systems perspective. We see an important role to be played by comparative psychologists in managing resources, increasing our activity in social and political issues, and transcending our traditional role as the study of animal behavior to one that makes significant contributions to psychology and humanity by studying relationships between animals and changing environments, and by providing a historical perspective on human evolution.*
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This is an article about the future of comparative psychology. Over the last three decades, comparative psychology has struggled with its identity as a psychological subdiscipline and in its relationship to other fields of psychology (Demarest, 1980; Hodos & Campbell, 1969; Wasserman, 1997). While this process has led some to express pessimism about the fate of comparative psychology, we see reason to remain optimistic about the future success and development for our discipline as we enter the new millennium. Our positive attitude is reinforced strongly by the appearance of three recent books: One is an edited volume, *Comparative Psychology: A Handbook* (Greenberg & Haraway, 1998) which provides coverage of the major areas of study in comparative psychology, the health of which is underscored by the more than 100 authors from five continents and 11 countries who participated in that project; the other two books are textbooks, *Comparative psychology: Evolution and development of behavior* (Papini, 2002) and *Principles of comparative psychology* (Greenberg & Haraway, 2002). These books describe a discipline that is vibrant and active, a still-developing field of psychology, not one in decline.

One view of the future of comparative psychology has been proposed by Wasserman (1997; Blumberg & Wasserman, 1995) and others (Hirsch, 1987), suggesting that we return to our roots—that of the study of mental continuity among the animal groups (Romanes, 1885). Comparative psychology thus envisioned is limited to the study of animal cognition. However, we perceive comparative psychology much more broadly to be the study of origins of *all* behavior, a *general* psychology if you will. Thus, we understand and conceptualize comparative psychology to be the study of the evolution and development of behavior of all organisms. While this may include cognitive processes and intelligence, such issues remain simply a part of the endeavor of the discipline rather than its major focus.

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The ''spiral staircase'' in our title refers to three categories of ideas and concepts that form the foundation of the position outlined in this article: DNA strands, coiled around each other in a spiral pattern, reflecting the contribution of biological factors to behavioral processes; the concept of levels of organization, which refers to the hierarchical nature of events in the universe; and the staircase leading up to the Department of Animal Behavior at the American Museum of Natural History, the incubator of many of the ideas presented here. The theoretical orientation espoused here is a synthesis of ideas drawn from J. R. Kantor's (1959; see also Pronko, 1980) interbehaviorism, Richard Lerner's (1998b) developmental contextualism, T. C. Schneirla's (Aronson, Tobach, Rosenblatt, & Lehrman, 1972) behavioral levels hypothesis, and Harry Helson's (1964) adaptation-level perspective. Additionally, we have been much influenced by the manner in which biologists such as Brian Goodwin (1994) and Stuart Kauffman (1993, 1995) elucidated the linkages between developmental psychobiology and newly emerging concepts of complex adaptive systems and self-organization (Prigogine & Stengers, 1984).

These somewhat diverse positions are linked by three crucial ideas: the important organizing principle of integrative levels, the idea that there is a tendency towards increased complexity with evolutionary advance, and the contextual nature of behavioral events. These ideas are embodied in a comparative psychology based on an anagenetic understanding of evolution and behavior and are fused within the framework of developmental dynamic systems theory. We have adopted a developmental perspective in which behavior is seen to be the result of the fusion of biological and psychosocial factors, by probabilistic epigenetic events rather than by preprogrammed genetic or other biochemical ones (Gottlieb, 1992, 1997; Kuo, 1967). Nonlinear dynamic systems theory provides a theoretically consistent language with which to describe and analyze behavioral development (Michel & Moore, 1995). Nonlinear dynamics contains a lexicon of concepts pertaining to change processes over time that does not exist in any other known theoretical system. Dynamical models allow us to compare and contrast seemingly unrelated phenomena that often share common dynamical structures. Dynamics explain aspects of phenomena that are not explained by conventional theory, either qualitatively or in terms of variance accounted for R-square, when people have framed their analyses along those lines (Guastello, personal communication, May 5, 2002). Nonlinear dynamics and complex systems analysis are continuing to help revolutionize our understanding in many of the life sciences in fields as diverse as molecular genetics (Wahde & Hertz, 2001), proteinomics (Metzler, Klafter, & Jortner, 1999), theoretical biology (Mikulecky, 1996), evolutionary processes of speciation (Bar-Yam, 1997), ecology (Wootton, 2001), and economics (Rosser, 1999), though these ideas are just beginning to find their way into mainstream psychology (Boker, 2001; Lerner, 1998a; Newell & Molenaar, 1998; Sulis & Trofimova, 2001).

The aim of this article is to provide an introductory overview of a theoretical perspective that we believe will solidify the role of comparative psychology as a field of study. Pursuant to this aim, we will first articulate several theoretical constructs which incorporate the somewhat diverse lines of thought discussed earlier and provide the foundation for our approach. Second, we will provide some exemplars of how this foundation has been implemented in understanding the evolution and development of behavior. We then conclude with a general discussion of how, by adopting this approach, comparative psychology functions as a general psychology by providing a foundation for other subdisciplines.

INTEGRATIVE LEVELS

We understand psychology to be a process-oriented science that operates at the interface of biological capacities and ecological contingencies. Thus, biological structure and function and their evolution are important behavioral participants from our perspective. Of equal importance, however, is the proximal ecological context in which an organism exists. In synthesizing these two ''causal domains,'' reductionistic perspectives are of limited value and an alternative conceptual paradigm is required. The concept of integrative levels provides such a conceptual framework.

The levels concept has a relatively long intellectual history in both biology (Brücke, 1861; Woodger, 1929) and functionalist psychology (Dewey, 1886; Morgan, 1901). The impetus for this line of thinking, which was common to all of these early theorists, was that the processes in both biology and psychology were qualitatively different from the structures and functions of less complex systems. Thus, biology needed an explanatory model distinct from physics and chemistry (e.g., Woodger, 1929), and psychology needed a model distinct from biology (Schneirla, 1949). The levels concept matured in the middle part of the 20th century through the notable work of scientists and philosophers such as Schneirla (Aronson et al., 1972), Needham (1929), Novikoff (1945), and Feibleman (1954). In its general form, the levels concept is a broad organizing principle regarding the temporal organization of matter as a series of discontinuous increases in complexity of organization. This can be seen in the definition of integrative levels so concisely summarized by Aronson (1984) as:

> . . . a view of the universe as a family of hierarchies in which natural phenomena exist in levels of increasing organization and complexity. Associated with this concept is the important corollary that these successions of levels are the products of evolution. Herein lies the parallel with anagenesis. (p. 66)

Using this broad definition, it becomes apparent that the sciences themselves have been divided into areas of study based on these qualitative changes in complexity of organization, with physics and chemistry addressing the lower levels of complexity and biology, psychology, and sociology addressing higher levels of complexity (see Feibleman, 1954).

In surveying the many formulations of the levels concept, several general defining principles emerge:

1. Complexity tends to increase over time.
2. There are thresholds of organizational complexity at which small quantitative increases result in qualitative discontinuities (i.e., levels).
3. The relationships between different levels of organization are nonlinear and probabilistically discontinuous.

Although the concept of integrative levels is a broad philosophical organizing principle, it has strong heuristic value when applied to a phylogenetic and ontogenetic understanding of behavioral origins. At a purely descriptive level, it provides a useful framework for disentangling phylogeny and ontogeny. Beyond pure description, however, the levels concept also is useful in generating meaningful and testable hypotheses regarding the relationships between biology, context, and developmental history in shaping behavior. As we have illustrated in a recent discussion of the origins of language (Greenberg, Partridge, Weiss, & Haraway, 1998), communication complexity is related to nervous system complexity, among other crucial factors. We ought not expect the simplest organisms to show more than simple means of communication, and we have every reason to expect that the most complex organisms with the most complex nervous systems will develop the most complex forms of communication. The answer to Deacon's (1997) question, "Why are humans the only species to have developed language?" is clear in this context.

The previous discussion shows that our proposal provides the primary theoretical foundation for a grade-based approach to comparative behavioral analysis. A deeper implication, however, has to do with the nature of scientific explanation. The concept of integrative levels, which is foundational to the perspective we are proposing here, provides an explanatory framework that is an alternative to reductionism. One of the primary postulates of the levels concept is that the phenomena of a particular level cannot be explained nor predicted by the phenomena or principles which apply at lower levels. Thus, the laws of each level must be unique to that level and cannot be derived from either lower or higher levels (Feibleman, 1954). It is not that lower level phenomena are unnecessary for understanding higher level properties. It is simply that the sum of actions of the lower level units is insufficient to explain the higher level behavior. While lower level behavior is involved in higher level behavior, it is mistaken to then conclude that higher level behavior is "nothing but" lower level behavior in aggregate.

The levels concept was derived primarily from empirical observation and philosophical deduction. The advent of nonlinear dynamics and the study of complex systems now provide a means to examine mathematically why these postulates have such strong utility. Indeed, in a discussion of reductionism in perceptual psychology, Uttal (1998) cited Moore's theorem that "No psychological, psychophysical, or behavioral experiment can ever say anything definitive about the internal workings of the mind or nervous system. It can only describe the course of the process, not what mechanisms account for it" (p. 46). He further asserts that the findings of chaos theory have demonstrated that Moore's theorem holds not just for the practical reasons of massive numbers of neural cells and the vast complexity of neural organization but rather it is true in principle because of the dynamics of that neural organization. What complex systems, such as those described earlier, have demonstrated is that molar system behavior cannot be reduced to molecular system component behavior.

ANAGENESIS

The position taken in this article agrees with Gottlieb's (1984) contribution to this discussion: "There is a theory in comparative psychology, and that theory is a hierarchical classification of adaptive behavior by grade [i.e., anagenetic analysis], independent of cladistic (i.e., genetic) relationship" (p. 454); and, "Anagenesis is of course not the only theory in comparative psychology, but it has been a major one since at least as early as the 19th century" (p. 449).

Anagenesis is the idea that there are directional trends in evolution, trends which reflect change from the simple to the complex. Let us avoid at the outset the highly charged and controversial idea in evolutionary thinking of "progress" by adopting Stephen Jay Gould's (1988) approach, that ". . . we can preserve the deep (and essential) theme of direction in history, while abandoning the intractable notion of progress" (p. 321). It is now undeniable from the fossil record that organismic

complexity has increased with time. Indeed, the evolutionary biologists Peter Saunders and Mae-Wan Ho (1976, 1981, 1984) suggested that increasing complexity is a second law of evolution after natural selection (for a thorough treatment of complexity in nature, see Chaisson, 2001).

In the context of the present discussion, these ideas relate to an anagenetic understanding of evolution, particularly as this applies to behavior. Anagenesis is a persistent idea not only in comparative psychology but also in comparative anatomy, comparative physiology, and comparative endocrinology (Yarczower, 1998). Textbooks in all of these disciplines routinely make comparisons between fish, frogs, turtles, alligators, pigeons, rats, cats, monkeys, and humans (Burghardt & Gittleman, 1990). Rather than being ''absurd'' (Hodos & Campbell, 1969), such comparisons can be useful, and even fruitful, depending on the questions being asked. As Tobach (1976) indicated, ''The choice of question and animal to be investigated depends on many factors other than nearness of evolutionary relationship'' (p. 197). We believe that this type of anagenetic analysis resolves the issue of ''capricious'' comparisons in comparative psychology which Hodos and Campbell and others have been critical of for more than 30 years. Crucial to this approach to analysis is the description of the criteria used to identify differences among higher and lower grades.

Behavioral Grades

While in the past the identification of grades as an ascending series of improvements had to be based on subjective criteria, it is now possible to propose two somewhat more objective criteria on which to base grade differences. The first relies on a biological and neurological approach; the second relies on a psychological and behavioral one. It is possible to rank species with respect to their brain complexity. This approach recognizes the significance of the relationship between brain and body size (Jerison, 1973, 1976, 1994), an objective dimension producing a measurable ''encephalization quotient'' based on structural attributes (Plotkin, 1983). This progressive encephalization quotient is understood to represent a greater capacity to process information (Olson, 1976), and improved information processing has long been recognized to be an important indicator of evolutionary advance (Pantin, 1951).

To the extent that the Transfer Index and learning set performance, measures of complex learning, follow an evolutionary trend (Rumbaugh & Pate, 1984), it is of interest to note that the encephalization quotient mirrors this trend. Related to this are the findings of Ridell and Corl (1977), who surveyed 23 species of mammals and compared them with respect to body weight, brain weight, number of cortical neurons, and their ranking on the ability to learn different complex problems. They reported high correlations among brain weights, number of cortical neurons, and problem-solving ability.

Our understanding of crucial factors in brain evolution are drawn from the ideas of Harry Jerison (1973, 1976, 1994), Terrance Deacon (1988, 1997), and others, who suggest that more evolutionarily advanced brains contain more neurons, and that this increased size permits greater integration and organization of sensory input. Larger brains are thus more complex, but rather than this increased complexity leading to disorder, it is an

> . . .'organized complexity:' the complexity which arises when a system of diverse parts bound together into an organic whole through numerous interactions, each of which has highly specific features. In such systems, the causal network for any particular property of the intact organism is often staggeringly complicated. (Seeley, 1995, p. 17)

Brain Complexity

A key concept in our formulation is that of a general evolutionary trend towards increased complexity, with nervous system complexity correlating highly with behavioral complexity. There are several ways of indexing brain complexity. One is to compare the relative proportions of Type I and Type II neurons, where Type I neurons form the primary sensory and motor pathways and Type II neurons are local circuit neurons which form central integrating circuits.

> The numbers of Type I neurons are closely correlated with body weight, whereas the numbers of Type II neurons are highly correlated with behavioral complexity. Thus from an evolutionary perspective, the ratio of Type II/Type I neurons increases as one ascends the phyologenetic scale. Similarly, increases in the ratio of brain to body weight, which one observes during phylogeny . . . probably result from this relative increase in the ratio of Type II to Type I cells. For example, the ratio of granule cells in the cerebellar cortex (Type II) to cerebellar Purkinje cells (Type I) is 1500:1 in humans, 600:1 in the cat, and 140:1 in the mouse. . . . (Benno, 1990, p. 118)

Related to this are species differences in neuron numbers in the hippocampus, an important structure in learning and memory. It has been shown that there is a continuous increase in both granular and pyramidal hippocampal cell numbers from rat to cat to monkey to man (Lassalle, 1996). These brain differences are reflected as well by behavioral differences, as the Transfer Index and learning set data previously referred to show. More advanced nervous systems function more efficiently,

reflecting the ''order for free'' idea introduced and discussed later.

It is safe to say that these progressive neural developments reflect phylogeny, are measurable, and thus are objective indices of increased complexity. These nervous system advances are reflected in a behavioral way as well, and we turn next to this way of assessing anagenetic change.

A Behavioral Taxonomy: Anagenesis Applied

Campbell and Hodos (1991) cited Demarest (1983), who portrays the anagenetic analysis of learning as a failure. However, Demarest offers no evidence for this point beyond merely stating that since learning does not leave fossils, we cannot discover its evolutionary course. However, Demarest said that in 1983; archeological methods have much improved since then, and it is now possible to go ''just as far beyond speculation about past behavior as can, say, a cognitive-development-psychologist when speculating about what might be going on in a child's mind. Perhaps even further'' (Mithen, 1998, p. 61). It is now recognized that the course of evolution endowed organisms with increasingly complex nervous systems, and as a result, more complex and plastic behavioral potentials (Dean, 2000; Gottlieb, 1997; Kuo, 1967; Mithen, 1996).

This useful approach to taxonomy (e.g., anagenesis) is labeled *pheneticism* by Harvey and Pagel (1991). In pheneticism, taxonomic position is decided by phenotypic similarity rather than by phylogeny. The levels concept suggests the ranking of animals with respect to their degree of behavioral plasticity. Animals less behaviorally plastic function at lower behavioral levels at which biological processes are of great significance; more behaviorally plastic organisms function at higher behavioral levels at which psychological processes (e.g., mediation) direct the course of behavioral development (see Hebb, 1949). We understand this increased behavioral plasticity to be a result of increasing nervous system advance, complexity, and organization. Tobach and Schneirla (1968) proposed a hierarchy of behavioral levels: taxis, biotaxis, biosocial, psychotaxis, and psychosocial. The utility of this idea was recognized as early as 1900 by Hachet-Souplet (Small, 1901) and has served as one of the themes of all T. C. Schneirla Conferences (Greenberg & Tobach, 1984, 1987, 1988, 1990, 1997; Hood, Greenberg, & Tobach, 1995). Gottlieb (1984, 1985, 1997) referred to this theoretical approach as behavioral analysis by grades, in which each new behavioral level is considered a new grade. We believe that the primary value of Tobach and Schneirla's taxonomy is its use as a conceptual framework for formulating hypotheses about behavioral evolution and development. We have used it as the basic organizing principle in our recent discussion of the full range of behavior across the animal kingdom (Greenberg & Haraway, 2002).

Anagenesis has been critically assailed in psychology (Campbell & Hodos, 1991). We have addressed those criticisms elsewhere (Greenberg, 1995) and see no reason to reiterate them here. Suffice it say, however, that while anagenesis may be of limited value in biology, we agree with Eldredge (1997) that it is an important conceptual tool for comparative psychology. Evolution is about change over long periods of time. Science speaks of cosmic evolution as well as of biological evolution. But the mechanisms appropriate to each are different. Cosmic change is not subject to the same principles of natural selection that apply to biological change. So, while the terms are the same, the mechanisms invoked are different. The same situation holds with respect to behavioral and biological evolution. As different sciences, we ought not expect the same principles to apply to both. This is an implication of the integrative levels concept. The point is that our adoption of an anagenetic perspective for behavioral change is consistent with this argument. We are not applying this concept to biological processes, but rather to psychological ones. And, this circumstance is strengthened by the compatibility of these processes with each other. We have recently shown how this perspective can foster our understanding of the evolution of complex behavior, of language, and of culture (Greenberg et al., 1998).

APPROACH/WITHDRAWAL HYPOTHESIS

T. C. Schneirla's approach–withdrawal (A/W) theory provides an example of how the principles we have described can be coalesced into a coherent theory of behavioral organization (Maier & Schneirla, 1935/1964; Schneirla, 1959, 1965). This is a general organizing principle that seeks to explain behavior in terms of biphasic processes based on stimulative characteristics and effects. The theory proposes three postulates: (a) The *maturation–experience principle*, in which maturation refers to the growth and differentiation of tissues and organ systems and experience to *all* stimulative effects upon the organism. This principle emphasizes the interrelatedness of structure and function in both phylogeney and ontogeny. In our usage, maturation and experience do not interact; that would imply that they were separate (though interdependent) developmental processes. Rather, following Schneirla, we see them as fused systems with no real line of demarcation between them. (b) The *levels concept*, which we have discussed at length earlier; and (c) the *approach/withdrawal intensity hypothesis*, which

states that early in an organism's life behavior is organized in such a way that low-intensity stimuli tend to arouse organic processes that result in approach responses while high-intensity stimuli tend to arouse organic processes that result in withdrawal responses, with respect to the source of stimulation.

Research has confirmed the validity of these postulates and shows that they can be successfully applied to a wide range of behaviors in many species (Chess & Thomas, 1990; Schneirla, 1965; Thomas & Chess, 1977; Turkewitz, Gardner & Lewkowicz, 1984). The theory has implications for the understanding of behavioral development in general.

Schneirla's (1957) conception of behavioral development is essentially an epigenetic one, though he did not specifically use that term: Behavior is not something an organism is born with but rather something it develops. Organisms which function at the different behavioral levels (discussed earlier) are characterized by different behavioral potentials (Kuo, 1967). The biological uniqueness of a species dictates that it interacts differently with its environment than do other species. Behavior arises as result of this interaction. As the organism changes (i.e., matures), its development is directed along one pathway or another. Changing maturational possibilities, then, changes the organism's final behavioral repetoire. ''This formulation corresponds to a fundamental concept of modern embryology according to which organism and development medium are inseparably related [i.e., fused]'' (Schneirla, 1965, p. 352).

DYNAMIC SYSTEMS

Although our theoretical approach has had proponents throughout the brief history of scientific psychology, many of its features have been difficult to empirically validate. Thus, many early systems theorists argued these principles in philosophical rather than empirical terms (Goldstein, 2000). Interestingly, there has been a parallel history in the study of nonlinear dynamic systems. Indeed, many of the fundamental mathematical assertions of contemporary nonlinear dynamics were first articulated in the late 19th century (Ruelle, 1991). However, these problems were analytically intractable until only recently. The advent of computers has resulted in an exponentiation of research into the qualitative behavior of mathematical nonlinear dynamic systems. Many of the concepts postulated by both the concept of integrative levels and nonlinear dynamic systems are operationally consistent. Thus, these new advances in nonlinear dynamics have provided a tractable methodology for expressing and validating the principles and hypotheses derived from the levels concept. Here, we provide discussion of three principles fundamental to the position we are espousing.

1. Complexity Increases Over Time

There are two historically consistent objections to this proposition. The first is that complexity cannot increase over time as this would violate the second law of thermodynamics. The second objection is that this claim is teleological and therefore lies in the realm of metaphysical pseudoscience. Nonlinear dynamics has provided a rebuttal to both of these objections.

The objection that increases in complexity violate the second law of thermodynamics at first glance appears to present a serious dilemma for the integrative levels concept. However, we certainly can see that there is much in nature that seems to be unaware that these violations are taking place. Biological systems in particular are quite adept at circumventing the second law. Species have tended to become more complex over phylogenetic time, and ontogeny can be defined as a process of increasing heterogeneity and organization (i.e., complexity). The answer to this paradox can be found in the study of far-from-equilibrium systems. While we sometimes talk of homeostasis and equilibrium in biology, in reality the equilibrium state for an organism is death. Rather, what we mean when we talk about biological homeostasis is the maintenance of coherence at a far-from-equilibrium state. Far-from-equilibrium systems maintain their coherence through a process of energy dissipation (Prigogine & Stengers, 1984). These systems require high amounts of energy to maintain their coherence and also create a significant amount of energy in this process, which must be dissipated back into the environment. One characteristic of dissipative systems is that they are characterized by increases in complexity (Lewin, 1992). A vital point here is that these systems do not increase in complexity for the purpose of being more efficient or some other teleological ''goal.'' Rather, the local dynamics of far-from-equilibrium systems interacting with their local environment result in increasing complexity. There is no purpose or goal or drive involved at all.

A second important feature of far-from-equilibrium systems is that they tend to be adaptive (Kauffman, 1993). An interesting phenomenon occurs as a result of this adaptive property. As the system becomes more complex, it becomes capable of interacting with more features of the local environment, thus the environment becomes more complex relative to the system operating within it. As such, as more complex organisms evolved, they were able to exploit more aspects of the environment, thus producing more and more niches to be filled. This soon becomes an iterative process in which complexity begets more complexity (see Bar-Yam, 1997).

2. There Are Thresholds of Organizational Complexity at Which Small Quantitative Increases Result in Qualitative Discontinuities (i.e., Levels)

Empirical validation of this aspect of the levels concept is now possible through one subfield of nonlinear dynamics referred to as catastrophe theory. In the mid-1970s, the study of discontinuity was greatly enhanced as a result of Renee Thom's (1975) catastrophe theory, which posits that all discontinuous forms or topologies can be described by one of seven elementary topological equations (see Guastello, 1987 for a review). These models are characterized by asymmetry parameters and bifurcation or splitting parameters. Asymmetry parameters are variables that function very much like predictor variables in standard linear regressions. As the value of the asymmetry parameter increases, the value of the dependent variable also increases in a smooth, linear fashion. The bifurcation parameter, conversely, is a variable which at some point "splits" the dependent variable from an n-modal distribution to a distribution with >n modes. For example, in the cusp catastrophe model (which is the most commonly employed form), the bifurcation variable will have a threshold at which point the dependent variable distribution will abruptly transition from a unimodal to a bimodal distribution. The initial difficulty with Thom's formulation of these topological forms was that they were very hard to parameterize; thus, the initial enthusiasm for catastrophe theory faded. However, recently several advances have been made toward successfully implementing these models (see Hartelman, van der Maas, & Molenaar, 1998).

3. The Relationships Between Different Levels of Organization Are Nonlinear and Probabilistically Discontinuous

Although closely related to Point 2 above, this principle relies much more strongly on the concept of emergence (Goldstein, 1999), often criticized as seeming to be somewhat mystical. Indeed, some have argued that invoking emergence is a sophisticated way of stating our ignorance (Henle, 1942). However, contemporary notions of emergence are grounded in materialist philosophies and invoke no metaphysical aspects. Further, rather than emergent properties being a temporary descriptor to be replaced by a more thorough reductionistic account, emergence is now considered to be "true" property of complex systems (Kauffman, 1993, 2000). Kauffman (1993) developed an abstract model of complex adaptive systems, which biological organisms are, that has proved useful in understanding how emergence arises from the internal dynamics of these systems. Kauffman's (1993) model, known as an NK model, is characterized by two parameters. The first is simply the number of components in the system, which is commonly notated by the parameter N. Second, there is the number of functional connections between each system component and other system components, which is represented by the notation K. Finally, there is the set of rules or transformations by which component behaviors at Time $t-1$ lead to the component behaviors at Time t (for a thorough introduction, see Kaplan & Glass, 1995).

These kinds of systems display three regimens of molar behavior. At low levels of interconnectivity, these systems have a tendency to become chaotic with very little, if any, component or system stability. At the other extreme of complete interconnectivity, where each component is dependent upon nearly all other components in the system, the behavior of the system becomes "frozen" into a static, unchanging system. A third state, and for our purposes the most interesting, is that of systems with a critical ratio of component number and component interconnectivity. At this critical ratio, the system displays molar level stability and microlevel instability. In other words, the behavior of individual components within the system is volatile, but the global "structure" of the system as a whole is stable.

This property of global stability and internal instability allows these systems, which Kauffman (1993, 2000) referred to as being "poised at the edge of chaos," to be quite adaptable to changing environmental pressures and contingencies making them ideal for flourishing under principles of natural selection. Another important dimension of these kinds of systems is that they can be autocatalytic or self-organized. Kauffman (1992, 1993) referred to these systems as demonstrating "order for free," because they require no external source of energy or information to achieve the highly complex and adaptive behaviors described earlier. In other words, when the parts of a system are organized in novel ways, new properties emerge as a result of that reorganization. In physics, this idea is fundamental to understanding the results of the Big Bang (Weinberg, 1977). In chemistry, mixing oxygen and hydrogen in the context of a spark yields water. In biology, this suggests that despite the 260 different cell types of a human being, the 30,000 genes each encoding a different protein, and the one quadrillion cells that form a newborn infant, the infant is a highly organized and integrated system. These ideas are being applied with surprising alacrity to psychology and especially to neuroscience (Hood, 1998; Vandervert, 1995). This spontaneous order "... is so powerful that it seems simply foolish or stubborn not to examine with the utmost seriousness the possibility that much of the order of ontogeny is spontaneous, crafted thereafter by selection." (Kauffman, 1995, p. 99). It has recently been suggested that these ideas are fundamental to understanding

physical, geological, biological, and behavioral systems and may indeed be a fundamental principle of all science (Bak, 1996).

There are several important implications of this point of view for understanding organismic behavior. A long-standing difficulty in psychology is understanding the relationship of behavioral phylogeny and ontongeny. As we argue here, historical trends toward increased neuro-architectural complexity and behavioral capacity need not be the result of "lucky genes" or a teleological process. Rather, as evolution led to more complex neurophysiologies, more neural integration was possible (e.g., Dean, 2000). The changes in behavioral capacity that seem to correspond with this increase in complexity and integration mirror the behaviors we find in dynamic systems. We see a similar process on an ontogenetic time scale, the difference being one of magnitude. The behavioral diversity over a life span is much smaller than that over an evolutionary time scale.

COMPARATIVE PSYCHOLOGY AS GENERAL PSYCHOLOGY

In a recent commentary on the history of comparative psychology, Dewsbury (2000) suggested that while comparative psychology played an important role in psychology's beginnings, it became a small and marginalized discipline in the latter half of the 20th century. Quite to the contrary, we assert that while comparative psychology proper has diminished in relative size, its contributions remain influential. Indeed, the theoretical postulates and methods of comparative psychology have become so integral to a such a wide array of psychological subdisciplines that the formal separation of those subdisciplines and their comparative dimensions seems capricious. As such, we see our approach to comparative psychology as a general psychology which informs and influences fields ranging from ethology to prevention.

Animal Behavior

Pisula (1998) recently showed how this approach to comparative psychology enables us to make sense of the enormously complex field of exploratory behavior, where there are still few agreements even to the precise definition of exploration. Figure 1 represents Pisula's approach to analyzing exploratory behavior from our grades or levels perspective. Depending upon one's level of analysis, both functions of and mechanisms underlying behavior vary. Figure 1 shows the variety of forms of exploratory behavior arranged hierarchically from the simplest to the most complex. Animals displaying the least complex forms of exploratory behavior, what Pisula labeled

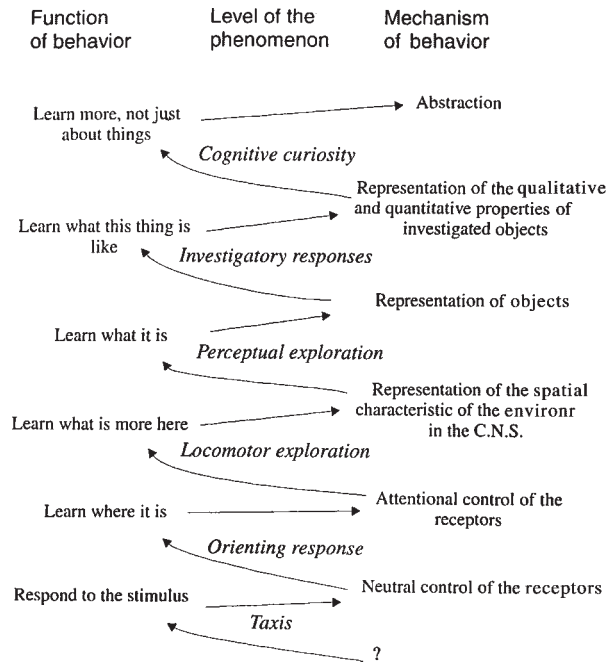

FIGURE 1 Levels of exploratory behavior. From "Integrative levels in comparative psychology—The example of exploratory behavior," by Wojiech Pisula, 1998, *European Psychologist*, 3, p. 66. Copyright 1998. Reprinted with permission.

"taxis," are at the bottom of this hierarchy, which lists increasingly more complex forms of exploratory behavior culminating in "cognitive curiosity" at the top of the hierarchy. As with other iterations of the use of our concept of behavioral grades, there is a correlation in this taxonomy with that used by evolutionary biologists. As can be seen in Figure 1, Pisula showed that behavioral functions of exploring become more complex, as do the controlling mechanisms, as we move from the simple ("lower") to the complex ("higher") levels.

As others have pointed out (Gottlieb, 1992; Thiessen & Vallarreal, 1998), given the anagenetic nature of the behavioral levels discussed previously, one can begin to ask questions about the proximate mechanisms underlying adaptive behavior, learning ability, or intelligence—mechanisms such as brain complexity. Thus, we see the idea of behavioral levels or behavioral grades as being an important heuristic, a significant result of which is enabling us to choose the right animal for the right comparative question.

Neuroscience

Many of the ideas we have presented have been incorporated into contemporary neuroscience. Notable among these are the organism–environment system theory proposed by Jarvilehto (1998) and Freeman's (1991, 1992) work on brain dynamics. The organism–environment

system theory asserts that the distinction between organism and environment is artificial and that one cannot understand the neurophysiological functioning of organisms independent of their ecological context. Likewise, the organism's ecology can be meaningfully understood only in relation to its neurophysiology. This idea is consistent with the integrative systems view articulated in our approach to comparative psychology.

Freeman (1991, 1992) has been one of the pioneers of applying systems notions to the study of brain functioning. In the examples of his work cited earlier, he implicitly utilizes many of the principles of organization and integrative levels that we have proposed here in understanding how we get complex brain dynamics from neuronal functioning. These ideas have led to a new understanding of how unintelligent agents such as neurons can, through aggregate behavior, lead to intelligent functions (also see Dean, 2000; Holland, 1996). Some of these ideas and formulations form the very foundations of contemporary neuroscience (Pribram, 1993, 1994, 1996). Uttal's (2001) critique of the localizationist hypothesis also incorporates a dynamic systems approach to neural functioning. Thus, rather than consisting of numerous independent cognitive modules, the brain is conceptualized as a dynamic set of circuits functioning as a unit.

Perception and Motor Development

The study of perceptual and motor development also has been imbued with many of the ideas we have proposed. The leading advances in this area of study focus on the origins of coherent patterns of motion through a dynamic coupling of independent functional units (Goldfield, 1995; Kugler, & Turvey, 1987; Thelen 1989, 1990). Many of the ideas such as emergence, integration of activity on multiple temporal and spatial scales, and self-organization are fundamental to our understanding of human perception and action. It is interesting to note that Gibson's (1966) ''ecological approach'' to perception is again in vogue.

Developmental Science

Over the past two decades, there has been a burgeoning of theoretical developments across a diverse set of disciplines including developmental psychology, sociology, developmental epidemiology, psychobiology, and embryology that have a common conceptual foundation—and in many cases, methodological approach—with the comparative psychology we have outlined here. While these theoretical formulations differ in specifics, they share a core set of common assumptions such that Bronfenbrenner has referred to these interdisciplinary advances as an ''emergent convergence and isomorphism'' (Cairns, Elder, & Costello, 1996, p. ix). Indeed, theoretical frameworks such as developmental contextualism (Lerner, 1998b), ecological (Bronfenbrenner, 1977), life span (Brim & Kagan, 1980), person centered (Magnusson, 1995), transactional (Sameroff, 1983), and developmental psychopathology (Cicchetti & Cohen, 1995) have such a degree of commonality that Magnusson and Cairns (1996) proposed incorporating them under the umbrella concept of developmental science.

One of the leading proponents of this movement is Richard M. Lerner (1998a,b,c), who has been quite active at both basic theoretical levels and at the policy-level applications of this perspective. The empirical research conducted by Lerner and colleagues (e.g., Talwar, Nitz, Lerner, & Lerner, 1991) focused primarily on the natural contextual shifts found in adolescence. For instance, the transition from junior high to high school connotes a significant shift in the contextual demands placed upon an adolescent. By studying the interaction of these contextual shifts with variables such as temperament, it can be shown empirically how these mutual influences not only shape each other but how they conjointly influence other behavioral outcomes.

Many scientists are already examining social behavior from a developmental contextual perspective. Building on the youth development work of Weiss and colleagues, Lerner (1995) described a Development-In-Context Evaluation (DICE) model for program design and evaluation as a framework for interventions addressing social problems. The DICE model explicitly incorporates program designs and policies as well as evaluation into the nested ecology of behavioral development. Indeed, not only are children and adolescents influenced by program design, implementation, and evaluation activities but they also directly influence those activities in a reciprocal manner. Additionally, multiple levels of a developmental system are assessed qualitatively and quantitatively at multiple levels of analysis.

Personality and Social Psychologist Albert Bandura (1989) put forth his belief that dynamically interactive, person context developmental models must become incorporated into the theory and research of personality and social psychology. Bandura explained the need for reliance on reciprocal effects in a triadic system of reciprocity among the person or organism, behavior or action, and the environmental or contextual influences. While Bandura recognized that current methods which investigate what he calls initial effects, or effects which do not rely on interactional assessment, are important to our understanding of development, he argued that to understand psychological functioning, our methods must include reciprocal as well as initial effects. Bandura also believed that, in a reciprocal system, change and context must take a primary focus if the field is to advance.

James Garbarino (1992) explained individual development as a process which occurs in the context of several different levels of influence. Like Lerner and Bandura, Garbarino stressed the importance of being aware of the changing contexts in which individuals develop, the changes over time in the individuals relationships to those contexts, and how individuals and contexts continually shape one another. The work of Lerner, Bandura, and Garbarino represents a trend evident across a variety of different researchers who examine individual and social systems problems away from simple cause and effect and reductionist models toward an approach to development which incorporates a developmental contextual perspective.

IMPLICATIONS FOR RESEARCH

The forgoing review is just a brief sampling of the many areas of psychological inquiry that are compatible with our perspective of comparative psychology. In addition to the research outlined earlier, a plethora of testable questions can be derived from this approach. For example:

- Is teaching of humans by humans the same as the apparently purposeful modification of behavior of young apes, birds, or rodents by the behavior of adults (Barnett, 1998; Tobach, 1995)?
- Do variations in maternal care affect the development of neuroendocrine responses to stress in rats (Liu et al., 1997), and do the same effects occur in humans (Sapolsky, Alberts, & Altmann, 1997)?
- What are the relationships between physiological reactivity, temperament, and caregiver attachment in humans (Fox & Calkins, 1993)?
- Does physiological reactivity and regulation of the neuroendocrine system influence developmental experiences (i.e., exposure to social behavioral cues) and vice versa?
- Does poverty influence embryological developmental of the neuroendocrine system?
- Can we determine allometric relationships between physical and behavioral characteristics?

Far from being simply a descriptive scheme, the perspective we have outlined in this article poses research questions that beg to be addressed:

1. If behavioral complexity and plasticity correlate with organismic and nervous system complexity, we can hypothesize that only the most complex species have complex communication systems. Bees, then, ought not be expected to possess a complex "dance language," and indeed, they may not despite nearly a century of acceptance of Von Frisch's hypothesis (Wenner, 1998). Their communication behavior may be based on simple sensory mechanisms (e.g., olfaction) rather than on some complex cognitive capability. This question is still an open one.
2. Similarly, monarch butterflies have been postulated to possess complex navigational skills beyond the capabilities of any other insect or butterfly species. The return of monarch butterflies from northern locations in Canada all the way back to Mexico, from whence their ancestors of several generations began a northern migration years before, has intrigued laymen and scientists alike. How do these butterflies find their way back to a place they have never been? How do they recognize landmarks in country they have never seen? Without landmark recognition, how do they navigate successfully across such vast distances? Many had assumed some type of cognitive process must be involved in the production of this impressive behavior. However, from a levels perspective, a more parsimonious explanation in accord with the position espoused here may explain this phenomenon. Recent observations (Marriott, 1999;Wenner & Harris, 1993) suggested the matter may have an explanation considerably more simple than anyone had previously imagined. Appraisal of all data available on monarch migration suggests to Wenner that the monarchs which manage a return to Mexico may simply have been carried there by prevailing winds. Passive flying under the influence of prevailing winds would be sufficient to deliver quite a number of migrating monarchs back to Mexico. After all, only a small proportion of the migrating population of monarchs actually accomplishes the return to Mexico. It is true that more monarchs tagged in the United States and Canada have been found in Mexico following migration than have been found in other directions, but almost no one has been looking for them in any other location. It also is true that monarchs in migration are often seen flying in the wrong direction—heading north rather than south.
3. These illustrations show that in addition to its descriptive utility, the levels concept can be used to generate many empirically testable hypotheses regarding complex behavior. For example, (a) bees communicate on the basis of olfactory rather than semiotic processes; (b) monarch butterflies do not migrate to Mexico but rather are passively carried by prevailing wind currents; (c) Tobach and Schneirla's (1968) discussion of behavioral levels discussed earlier intended to apply this hierarchy to social behavior alone. However, we have seen it a useful way to conceptualize much broader categories of behavior. In our recent book (Greenberg & Haraway, 2002), we attempted, admittedly somewhat incompletely, to apply this hierarchy to other categories of behavior, most fruitfully to

feeding and language. The levels scheme, while useful, is still premature and subject to revision; we wonder whether other researchers can apply this conceptual scheme more broadly to other categories of behavior. We believe this to be useful in further developing the unified theoretical perspective we are presenting here.

4. Finally, while Schneirla (1959, 1965) proposed the approach/withdrawal principle as a ''theory,'' we understand it to be more a lawlike statement (Greenberg, McCarthy, & Radell, 1991). One persistent problem with respect to the stimulus intensity hypothesis relates to the intractability of defining the dimension of intensity. We are comfortable proposing an objective approach in which the stimulus is defined in terms of its ''complexity,'' a more complex stimulus being considered a more intense one, complexity in turn being defined in information terms as ''bits of information'' (Attneave, 1957). The utility of this approach has been recognized and discussed by Walker (1980), who extended the notion to a wide array of behavioral situations.

One prediction that can be made from this idea is that young animals will spend more time in the presence of low-intensity stimuli than they will in the presence of stimuli of high intensity. Work we have completed provides only the most preliminary test of this hypothesis, but those results are intriguing and suggest numerous directions for further evaluation. For example, we were able to demonstrate that two closely related rodent species, gerbils (*Meriones unguiculatus*) and spiny mice (*Acomys russatus*), seem to spend more time in the presence of ''less complex'' visual and haptic stimulation (Greenberg et al., 1991). If these results are replicable and can be extended, they go a long way toward demonstrating the broad application of the approach/withdrawal hypothesis.

CONCLUSIONS

As we stated in our introduction, we intended in this article to counter the pessimism displayed by many contemporary comparative psychologists by spelling out and defending a methodological and conceptual foundation for comparative psychology with which to enter the millennium. Despite recent efforts to diminish the presence of comparative psychology within the American Psychological Association by proposing to eliminate that term from the title of Division 6, the division is presently called, *Behavioral Neuroscience and Comparative Psychology.* That discussion not only strengthened our belief in the well-being of the discipline but is proof to us of the strong position we find ourselves in at the beginning of the 21st century. We have identified here the widespread adoption within all of psychology of many of the ideas, concepts, and empirical findings generated by comparative psychology in over 100 years of study.

Rather than taking the position suggested by Wasserman (1997) that we narrow the scope of comparative psychology to ensure its survival, our advice is to do the opposite and broaden our scope. Comparative psychology today is not only about drosophila, gerbils, and animal cognition but about *Homo sapiens* as well. As the principal players in the survival of the biotic and abiotic environments, the understanding of human behavior becomes crucial (Tobach, 1988, 1991). This suggests an added role for comparative psychology: management of resources and increased activity in social and political issues. In this role, research by comparative psychologists could be conducted in the context of current ecological and social crises. As Ethel Tobach stated in her address to the 4th biennial meeting of the International Society for Comparative Psychology, 1988, in Sydney, our discipline would then transcend its traditional role as the study of animal behavior to one that makes significant contributions to resolving critical issues relating to the relationships between animals, humans, and our changing environments (Innis, 2000). It is fitting that we end this article on that note, especially given the title of Tobach's address, ''Comparative Psychology in the 21st Century.''

NOTE

This article is based on the first author's Division 6 Invited Fellow's Address at the annual meeting of the American Psychological Association, Chicago, August, 1997.

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