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ANAGENETIC THEORY IN COMPARATIVE PSYCHOLOGY

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ABSTRACT: This paper is a response to Campbell and Hodos' continuing critiques of the field of comparative psychology. Their opinion to the contrary, I show that anagenesis is still a useful concept to evolution scientists and that anagenetic analysis provides a viable and fruitful approach to theory development in comparative psychology. Anagenesis suggests improvement with evolution and the idea of complexity as an indicator of evolutionary progress is discussed. Finally, the paper discusses the utility of a modified form of the *Scala naturae*, namely the concept of integrative levels by showing how T. C. Schneirla has used this idea as the foundation of his significant theoretical contributions to comparative psychology.

INTRODUCTION

In their widely discussed critique of comparative psychology, Hodos and Campbell (1969) indicted the field on the grounds that it was not based on a valid theoretical orientation. They asserted that comparative psychologists misunderstood evolutionary theory, citing its long history of capricious comparisons, i.e., comparisons of behavioral differences among animals that do not represent "true" evolutionary lineages. Needless to say, their paper generated a substantial response (e.g., Gottlieb, 1976, 1984; Tobach & Adler, 1974). The argument was made that Hodos and Campbell were wrong, that comparative psychology was indeed guided by theory, evolutionary theory, and that the *Scala naturae*, while dated and outmoded, still offered some important guidance in making generalizations about evolution and behavior. Their critical commentary has continued to the present (Campbell, 1976;

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Campbell & Hodos, 1991; Hodos & Campbell, 1990).

I am reminded of what the late Harry Helson told us as graduate students: that as editor of the *Journal of Experimental Psychology* he did not enter debates such as this because he believed they did not contribute to scientific advance. Indeed, the present debate has been characterized as being "acrimonious" (Gottlieb, 1984). I do believe, however, that continuing this dialogue in a constructive manner can be useful in helping us redefine and refine our formulation of the significant questions that need to be asked about behavior and evolution. The most recent focus of this debate is the continued use within comparative psychology of "anagenetic analysis" (Campbell & Hodos, 1991; Hodos & Campbell, 1990). A related issue is the utility of an hierarchical perspective.

The position taken in this paper 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).

Some comparative psychologists have proposed the concept of anagenesis be used as an alternative formulation of the evolutionary scale (e.g., Gottlieb, 1984; Yarczower, 1984; Yarczower & Hazlett, 1977; Yarczower & Yarczower, 1979). Campbell and Hodos (1991) find fault with anagenesis because of a failure among evolution scientists to agree on its definition. Nevertheless, while there has been disagreement as to whether anagenetic changes occur within grades or clades (Gottlieb, 1984), whether they apply to changes in parallel or convergent evolutionary processes (Yarczower & Hazlett, 1977), or whether such changes reflect our own anthropocentric views of the universe (Huxley, 1942, 1957), the concept still plays a role in discussions of evolution (e.g., Devillers & Chaline, 1993; Futuyma, 1987; Gould & Eldredge, 1993; Panchen, 1992). Current usage appears to uniformly refer to progressive evolutionary change (Davey, 1989; Panchen, 1992, 1993: Scott-Ram, 1990).

In expressing their concerns about anagenesis, Hodos and Campbell (1990) join a long list of scientists in pointing out the difficulty of satisfactorily defining evolutionary progress, the ongoing discussion of which is as old as Darwin's ideas themselves (Richards, 1992). Many, including this author, see merit in identifying evolutionary progress with increasing complexity and level of organization (e.g., Bonner, 1988; Dobzhansky, 1955; Lewin, 1992; Pantin, 1951; Stebbins, 1969; Wesson,

1991). An increasingly common approach to complexity equates it with improved information processing associated with nervous system evolution and advance (Jerison, 1994; Lewin, 1992).

While at one time it could be said that the concept of complexity had been neither adequately nor accurately treated in biology (Pringle, 1951), this is no longer the case (Wicken, 1984). In the first of a series of papers, Saunders and Ho (1976, 1981, 1984) presented an argument for the use of the dimension of "complexity" as a measure of progress in evolution, contending that it is:

> ...*the fundamental parameter in evolution.* An obvious advantage is that there is *no difficulty in defining it*; von Neumann (1966) defined complexity of an automaton to be the number of components it contains and there does not appear to have been any serious disagreement with this choice, although for biological systems a better measure is the number of different types of components.... *Increase in complexity is also comparatively easy to observe*, so we have a practicable partial ordering of species.... [I]ncrease in organization... is a secondary effect and comes about simply because the more complex a system is, the more organization it needs to survive...."(p. 377, italics added)...."[I]n our view there are *two* separate laws of evolution, survival of the fittest and *increase in complexity*.... (p. 383, italics added)

Indeed, there are now even "sciences of complexity" including ecology, economics, cognitive psychology and artificial intelligence (Lewin, 1992; Wesson, 1991).

This concept of progress in evolution is consistent with the important theoretical concept of integrative levels (Feibleman, 1954; Needham, 1943; Novikoff, 1945; Redfield, 1942) that Aronson (1981, 1984) has proposed be used as the basis for comparison in comparative psychology. The levels concept, he said:

> ... is 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. (1984, p. 66)

Again, Hodos and Campbell (1990) have rejected this argument, seeing no essential differences between the levels concept and anagenesis.

In contemporary usage, anagenetic analysis implies "improvement" with evolution (Panchen, 1992), hence the connection to the *Scala naturae*, which is alleged to have no place in contemporary science (Campbell & Hodos, 1991; Hodos & Campbell, 1969, 1990), although there is not universal agreement about this. Gould (1976), for example, says:

> ...it seems as though comparative neurologists remain rooted to Lamarck's *scala naturae* - for they persist in studying a fish, a reptile, an insectivore, a tree shrew, a monkey, and a man and in drawing from such comparisons a set of conclusions about vertebrate evolution... Paleontologists then seem to

> assert that because the series does not reflect true descent, it cannot designate anything of value. I propose ... that *this procedure, nonetheless, is both valid and valuable; and ... that it reflects an evolutionary concept of undoubted respectability*, despite its inevitably subjective basis (p. 115, italics added.)

Such reasoning is likely responsible for the persistence of comparisons among such "typical" animals as fish, frogs, turtles, alligators, pigeons, rats, cats, dogs, monkeys and humans in current textbooks in many of the sciences -- comparative anatomy, comparative physiology, comparative endocrinology, etc. (Burghardt & Gittleman, 1990). It is of interest to note that evolution scientists are not of one mind on the respectability of the idea of "progress." Gould's (1994) strong position on evolutionary progress is not shared by all evolution scientists and may reflect an ideology (Lewin, 1992). Indeed, according to Preuss (1995), the idea that brain evolution reflects a progressive trend towards improved information processing is a traditional way of thinking in neuroscience and psychology:

> That is to say, the pattern of brain evolution has been likened to a unitary scale or ladder rather than to a branching tree (p. 1230)

Hodos and Campbell (1969) began this debate by rejecting comparative psychology's use of some form of the evolutionary scale because it does not in any way represent a true historical lineage. Using the the work of Bitterman (1965 a,b) as an illustration, they have called such comparisons capricious (p.349) and absurd (1990, p. 1). This, however, loses sight of the fruitfulness and success of this approach as the following statement by Tobach (1976) underscores:

> Depending upon the question being asked, and the level of organization under investigation, the comparison [between mouse, rat, cat and monkey] is extremely fruitful... [particularly] in view of the fact that at this stage of knowledge there is no one criterion that has proved to be the most significant in determining the species to be compared. It has been said that if the tests for toxicity of thalidomide had been carried out on sea urchin eggs instead of adult mammals, the drug would not have been passed on for general use. The choice of question and animal to be investigated depends on many factors other than nearness of evolutionary relationship. (pp. 196-197)

A similar argument has been made by biologists as well. Wood (1972), for example, argued that, despite their distant evolutionary relationships, toxicity tests on rodents can provide quite valid indications of human reactions. Thus, it seems clear that such comparisons are not absurd but they can be quite useful.

Davey (1989) recently suggested that anagenetic analysis by grade provides a solution to the criticisms of Hodos and Campbell (1969) about "capricious" comparisons. Such analysis requires the elucidation of the (subjective) criteria used to identify different grades. His preference is to define grades as ascending series of improvements

which he illustrates with two much cited examples. The first approaches the definition of higher grades from a physiological perspective in which species are ranked with respect to the relationship between brain and body size (Jerison, 1973, 1994). This produces an objective measure, the encephalization quotient, "a true dimension based upon objectively measured structural attributes" (Plotkin, 1983, p. 128). Olson (1976) showed the relationship of this progressive encephalization quotient to represent a greater capacity to process information. A similar argument was presented by Killackey (1990) in his discussion of neocortical expansion and improved information processing which follow phylogenetic lines. Improved information processing was earlier recognized by Pantin (1951) to be a crucial indicator of evolutionary advance.

Davey's (1989) second example is Hölldobler and Wilson's (1983) description of progressively improved nest construction by some formacine ants in which higher grades are represented by improved adaptational strategies. Other examples include Razran's (1971) formulation of a hierarchical arrangement of learning capacities through eleven levels from "habituation and sensitization" to "thinking" and the discussion of "learning sets" in which evolutionary (phylogenetic) trends have been identified (e.g., Warren, 1965).

Campbell and Hodos (1991) cite 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 can not discover its evolutionary course. It has, however, been long recognized that it is the organism rather than its behavior which evolves (e.g., Tierney, 1986), the course of evolution endowing organisms with increasingly complex behavioral potentials (Kuo, 1967).

This useful approach to taxonomy is labeled *pheneticism* by Harvey and Pagel (1991). In pheneticism, taxonomic position is decided by phenotypic similarity rather than by phylogeny. One successful theoretical formulation from this perspective is that developed by T. C. Schneirla (Aronson, Tobach, Rosenblatt & Lehrman, 1972), whose description of "behavioral levels" represents a somewhat less subjective approach to defining successive grades as do the foregoing examples. Gottlieb (1984, 1985) has referred to this theoretical approach as behavioral analysis by grades, in which each new behavioral level is considered a new grade. In principle, taxonomy has always been somewhat subjective and arbitrary (Barnes, 1984; Brooks, 1983; Goldsmith, 1991; Gould, 1982; Harvey & Pagel, 1991; Miles & Dunham, 1993; Simpson, 1961; Sokal, 1974) so many orderly

arrangements are possible, including that proposed by Schneirla. It is of some significance to note that while Eldredge (in press) indicates that the concept of "grade" is little used among contemporary evolutionary biologists, he identifies Schneirla's use of the concept as an important explanatory tool for comparative psychology.

The levels concept, which serves as the cornerstone of Schneirla's theory (1949, 1953), 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. Increased behavioral plasticity is 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 of the T. C. Schneirla Conferences (Greenberg & Tobach, 1984, 1987, 1988, 1991, in press; Hood, Greenberg, & Tobach, in press).

The hierarchy proposed by Tobach and Schneirla (1968) should not be considered complete; it is rather an initial attempt at bringing order to behavioral comparisons. For example, as originally proposed, primates were ranked at the highest behavioral level, the psychosocial. However, combining all the primates into a single level ignores the enormous diversity and richness of primate behavior. For example, it is now widely believed that apes, and especially chimpanzees, are capable of true linguistic processes (Savage-Rumbaugh, Murphy, Sevcik, Brakke, Williams & Rumbaugh, 1993), though at a level substantially less complex than in *Homo sapiens*. This suggests grade differences between language and non-language using primates and *Homo sapiens*. I propose a refinement of the originally proposed single psychosocial level into three: Psychosocial 1 (includes all non-language using primates), Psychosocial 2 (language using apes), and Psychosocial 3 (*Homo sapiens*). While she alluded to this type of analysis in a recent discussion of animal cognition, Tobach (1987) went no further than drawing attention to the utility of a levels orientation in thinking about language processes. This approach is useful, too, in comparing learning capacities among the primates in an evolutionary framework (e.g., Rumbaugh & Pate, 1984).

It should be emphasized that the criticisms of Hodos and Campbell are not uniformly shared by all evolution scientists. No one can claim to have the final answer in this debate, including the present author. It is

my hope that Hodos and Campbell would agree with this point. A constructive attitude about this is reflected in Ho and Saunder's (1984) admonition that:

> It must not be supposed however, that there is anything approaching the 'consensus' which is often claimed for the neo-Darwinian synthesis. Pluralism is a predominant feature of the [*still*] emerging paradigm of evolution. Not only is there a genuine (and in our view, healthy) diversity of opinion and emphasis, but evolution is a complex phenomenon and it is to be expected that different kinds of explanations will be appropriate to different aspects. Thus, pluralism ought in principle to be a permanent feature of evolutionary studies. (p. 5)

Along these same lines, Gottleib (1984) has said:

> Although one cannot disagree with the factual basis of Hodos and Campbell's claim about evolutionary lineages, one can question whether their understanding of the terms *evolutionary* and *phyletic* is rather too narrow, not only for comparative psychology but for evolutionary biology as well... (p. 448).

This debate began in 1969 with the charge by Hodos and Campbell that there was no theory in comparative psychology. In response I have tried to show that Schneirla began the important task of building a comprehensive theory of behavior; his students and colleagues have undertaken the empirical work which has led and still is leading to the discovery of principles and laws upon which that theory rests. While it was unfortunate that Schneirla died when his theory was still incomplete, his ideas continue to influence researchers in comparative and developmental psychology. In this context I find merit in Harvey and Pagel's (1991) defense of pragmatism in the search for truth, especially when intellectually challenging ideas are involved. I have tried to show, as have others before me, that this debate can be useful and that denying the existence of valid theory in comparative psychology is shortsighted.

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