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3 Evolution and Learning Before Thorndike: A Forgotten Epoch in the History of Behavioral Research

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Contemporary accounts of the history of the study of animal learning frequently begin detailed consideration of the field with discussion of the work of E. L. Thorndike (see, for example, Bolles, 1975; Jenkins, 1979). It is not at all a bad place to start. Thorndike's (1898) publication of *Animal Intelligence* marks a turning point in the field of animal behavior generally and the study of animal learning in particular, replacing precedent anecdotalism and informal description with controlled experiment and laying intellectual foundations for decades of subsequent research in animal experimental psychology.

Strangely, one of the most radical departures in Thorndike's approach to the study of animal learning has not, so far as I know, been previously noted. Thorndike (1898) was the first scientist publishing after 1859 to write a major text on any aspect of animal behavior without mentioning Charles Darwin or the theory of evolution. Perhaps in consequence, it has become customary in histories of animal learning largely to ignore the fact that prior to Thorndike's emergence as a dominant figure in the field, study of associative processes in animals was an integral part of the study of evolution. Understanding learning processes was treated as essential to understanding of evolution and understanding evolution was, conversely, considered essential in interpreting learning capacities in animals.

The period from 1855 to 1898, when study of animal learning and study of evolution were integrated, was no golden age. In retrospect, the latter half of the 19th century appears a period of profound error in the study of animal learning, when overcommitment to predictions deduced from evolutionary theory of the day yielded very questionable science. It is, of course, easy to look back from the vantage provided by decades of additional research and discern errors in the

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contributions of our predecessors. It is more difficult to discern why those working in a period when evolutionary and behavioral sciences were less well developed than they are today reached the conclusions they did.

Following, I discuss a variety of related topics bearing on study of animal learning and evolution during the latter part of the 19th century: The controversy between Darwin and Wallace over the continuity of animal and human mind that motivated much of the 19th century study of learning in animals; Darwin's theory of Pangenesis, his ambiguity concerning the possibility of Lamarckian inheritance, and Weismann's rejection of the Darwinian position; the alternative models of phylogeny proposed by Spencer and Darwin; the views of Darwin, Wallace, Romanes, and Morgan concerning both the evolution of instinct and the role of observational learning in the development of instinctive patterns of behavior. Each played a fundamental role in shaping early studies of animal learning and each contributed to Thorndike's eventual rejection of the use of evolutionary models in the study of learning processes. Consequently, each had profound implications for subsequent developments in animal experimental psychology.

DARWIN AND WALLACE: THE CONTROVERSY

Alfred Russell Wallace's name is widely known as coformulator of the theory of evolution by natural selection. Often, as one reads brief histories of evolutionary thought, one is left with the impression that Wallace's sole contribution to the biological literature was the manuscript he sent to Darwin in June of 1858 that precipitated publication of *The Origin of Species*. Yet Wallace, like many other 19th century scientists, was a prolific author, publishing on a range of topics and espousing his own interpretation of the evolutionary process.

Although both Darwin and Wallace were committed to an evolutionary account of the origin of species, they differed considerably in the theories of evolution they proposed. Most relevant to the present discussion is the disagreement between them concerning the phenotypes that could evolve by the action of natural selection. As a contemporary, George Romanes (1884), stated the following concerning the major issue that divided Darwin and Wallace:

We all know that while Mr. Darwin believed the facts of human psychology to admit of being explained by the general laws of evolution, Mr. Wallace does not believe these facts to admit of being thus explained. Therefore, while the followers of Mr. Darwin maintain that all organisms whatsoever are alike products of a natural genesis, the followers of Mr. Wallace maintain that a distinct exception must be made to this general statement in the case of the human organism; or at all events in the case of the human mind. Thus it is that the great school of evolutionists is divided into two sects; according to one the mind of man has been slowly evolved from the lower types of psychical existence, and according to the other the mind of man, not having been thus evolved, stands apart, *sui generis* from all other types of existence. (p. 9)

Wallace's difficulty in attributing the development of the human mind to the action of natural selection resulted, first, from his commitment to natural selection as the sole mechanism of organic evolution and, second, from his conviction that the process of natural selection could produce only those morphological adaptations and behavioral capacities necessitated by the immediate demands of the environmental niche a species occupied. "No organ, no sensation, no faculty arises before it is needed, or in greater degree than it is needed. This is the essence of Darwinism" (Wallace, 1916, p. 404). In Wallace's view, if members of any species exhibit some capacity that exceeds the needs of that species in its natural habitat, evolution of that capacity could not be attributed to the action of natural selection.

Although Wallace fully accepted Darwin's conclusions as to the descent of man's bodily structure and brain from an ancestor common to ape and man, he rejected the hypothesis that either man's intellectual faculties (such as a musical or mathematical ability) or moral sense could have evolved by natural selection (Wallace, 1870, 1889).

Wallace had traveled widely in South America and the South Pacific as a naturalist and collector of exotic specimens. His observations of native peoples had convinced him that the intellectual and moral faculties required by the aboriginal way of life were not markedly different from those needed by mammals generally to survive in their respective ecological situations. Yet aborigines brought to England and educated there had the capacity to acquire the behavioral sophistication of modern Europeans. Thus, aborigines had moral and intellectual capacities far exceeding the immediate requirements of the environments in which they had evolved. Therefore the intellectual capacities of primitive man, and by implication modern man, could not be the result of natural selection.

This question of the continuity of animal and human mind was the great psychological issue of the last part of the 19th century. It motivated the initiation of the systematic study of comparative animal behavior and led via indirect paths to the form of animal learning theory we know today.

DARWINISM IN 19TH CENTURY PERSPECTIVE

The modern neo-Darwinian theory of evolution is an amalgam of disparate elements. At its center rest Darwin's notions of descent with modification and differential reproductive success. Equally critical to contemporary evolutionary theory are discoveries unknown to Darwin: Mendelian particulate genetics, Weismann's central dogma, Morgan's mutations, etc. Darwin's great genius (and his remarkable good luck) was that in the absence of requisite background information, particularly in the field of genetics, he was able to see, at times clearly, at others less well, the major features of the evolutionary process as we understand them more than 100 years after his death. In retrospect, it is easy to separate the wheat from the chaff in Darwin's published work on evolution. In the 19th century, the distinction was not so clear.

Darwin, in the view of his contemporaries, was the proponent of two competing theories of evolution, one based on natural selection, the other on the mechanism of heredity Darwin called Pangenesis. While Darwin's views on the importance of natural selection in evolution are universally known, his advocacy of the theory of Pangenesis is all but forgotten; unfortunately, it was the latter rather than the former that captured much of the attention of his immediate intellectual heirs. There is no need to go into the details of a disproven hypothesis, but, in brief, the "provisional hypothesis of Pangenesis," as Darwin (1868) termed it, stated that the cells of multicellular organisms throw off minute "gemmules" that collect in the reproductive organs. These gemmules form sperm or ova, packets of gemmules from all the cells of an organism, that, after fusion during reproduction, are capable of developing into somatic cells like those from which they originally derived. Most important to 19th century evolutionary theorists, the production of gemmules was held by Darwin to occur at all stages of life and the characteristics of individual gemmules to depend on the condition of their parent cells at the time they emitted gemmules.

Darwin, through the six editions of the *The Origin* he published from 1859 to 1878, generally held to the position that the random heritable variation observed in natural populations, on which natural selection acts to produce adaptation, is both unoriented with respect to fitness and of unknown origin. Yet the temptation must have been great to attribute naturally occurring heritable variation to effects of experience on the material entering into the reproductive process via the gemmules. Clearly there were profound effects of use or disuse of organs on the morphology of individuals. Also, it was obvious that individual organisms could modify their behavior. Darwin's own Pangenesis theory permitted experientially induced viariation in morphology or behavior to become heritable and thus open to selection. Evidence that such could not be the case was not available, yet Darwin was clearly reluctant to accept the Lamarckian inheritance his Pangenetic hypothesis permitted. Perhaps he realized that if acquired modifications of brain or body structure were heritable, the variation upon which natural selection acts would be directed and not random. Natural selection, the evolutionary process which Darwin studied for most of his adult life, would be relegated the relatively minor role of weeding out the less fit among adaptive variants, rather than creating adaptation out of random variation.

Darwin's contemporaries surely recognized the evolutionary implications of his Pangenetic hypothesis; they saw that, though ostensibly a theory of inheritance, Pangenesis bore the seeds of a theory of evolutionary mechanism that could largely supplant natural selection. "The theory of gemmules can freely

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entertain the doctrines of Lamarck'' (Romanes, 1893, p. 104) and because the action of Lamarckian inheritance ''must always have been *directive* on the one hand and *cumulative* on the other . . . [its] influence in determining the course of organic evolution may have been immense'' (Romanes, 1893, p. 107). Wallace, as mentioned above, was clearly committed to a strict selectionist view of the evolution of morphology and behavior in animals, but he was practically unique in his single-minded advocacy. Most of his fellow evolutionists, while accepting a role for natural selection in evolution, were considerably more taken with Darwin's Pangenetic alternative, especially when discussing the evolution of adaptive behavior.

VIEWS OF PHYLOGENY: DARWIN AND SPENCER

In the first edition of *The Origin of Species,* Darwin (1859) provided not only a materialistic explanation of the evolution of adaptation via natural selection, but also an account of the process of speciation as the result of natural selection acting in disparate environments over successive generations to increase divergence in characteristics of isolated populations. Darwin conceived of all organisms as descended from a common ancestor by a continuous process of branching that explained the varying degrees of resemblance among the forms of life on earth both extant and extinct. As Darwin (1859) so eloquently wrote:

> The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. . . . The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs; and this connexion of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinanate to groups. Of the many twigs which flourished when the tree was a mere bush, only two or three, now grown into great branches, yet survive and bear all the other branches; so with the species which lived during the long-past geological periods, very few now have living and modified descendants. From the first growth of the tree, many a limb and branch has decayed and dropped off; and these lost branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only from having been found in a fossil state. . . . As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (pp. 120–130)

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The important concept emerging from such a view is that extant species, while related to one another as are cousins of varying degree, are not linearly related as grandparents of varying degree are to their grandchildren. The linear forebears of contemporary species, genera, etc., long extinct, are observable only in the geological strata of past ages.

Darwin's view of the historical relationship among the myriad forms of life on earth was not the sole contender for scientific consideration in the latter half of the last century. Four years prior to the first printing of *The Origin of Species,* Herbert Spencer (1855) published a two volume work, *Principles of Psychology,* in which he provided an alternative evolutionary view of the relationships among extant species. It was a view that was to have a more profound impact than Darwin's on the study of the behavior of animals during the succeeding 100 years.

The two central concepts in Spencer's *Principles,* borrowed, perhaps unknowingly, from Aristotle, are, first, that the living world is continuously changing and, second, that the direction of this change is from simple to complex. In Spencer's view, each multicellular organism began life as a simple, relatively undifferentiated embryo and developed during its life into a highly differentiated being composed of specialized, interdependent parts. In an analogous fashion (and here Spencer departed radically from Aristotle), the living world began with a few simple forms of life from which increasingly complex forms evolved. To Spencer, such evolution meant steady linear progress from simple to complex, from lower to higher, from imperfect to more perfect. The history of life was to be viewed as a linear progression from the simplest unicellular organisms to man. Gradually increasing physiological complexity reflected in increasing sophistication of mind and behavioral efficiency was, in Spencer's view, a fundamental law of nature. The main difficulty came in Spencer's insistence that extant species could be linearly ranked using a criterion of increasing complexity in physiological and behavioral elaboration. "From the lowest to the highest forms of life, the increasing adjustment of inner to outer relations is one indivisible progression" (Spencer, 1855, Vol. 1, p. 387).

The notion of a smooth linear increase in the complexity of extant organisms surely did not originate with Spencer, but Spencer provided an evolutionary rather than a theological rationale for the existence of a Great Chain of Being or *scala naturae.* Spencer's linear model of phylogeny was treated as a serious evolutionary alternative to Darwin's branching model by their contemporaries. Spencer's model was consistent with the notion of a continuity of animal and human mind, but required, as Darwin's branching model did not, that this continuity would be directly observable in living species. Darwin realized that even within historical lineages extant species would not form a continuous, graded hierarchy. "A really far greater difficulty is offered by those cases in which the instincts of a species differ greatly from those of related forms. . . . But we should never forget what a small proportion the living must bear to the

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extinct'' (Darwin, in Romanes 1884, p. 378). His contemporaries failed to heed his admonition.

GEORGE ROMANES: DARWIN'S DISCIPLE?

As discussed above, to Romanes and others of his generation, Darwin and Wallace were advocates of strikingly different positions. Wallace was a strict selectionist, Darwin the proponent of both natural selection and Lamarckian evolution. Wallace denied the continuity of animal and human mind, Darwin affirmed that continuity. Romanes' life work was a defense of the Darwinian orthodoxy against Wallace's apostatic views.

Romanes has been perceived as he presented himself, as an intellectual champion of Darwinism. Consequently, those working in comparative psychology have traced their intellectual heritage to Darwin, using Romanes as the major link between comparative psychology and the theories of the founder of evolutionary biology (see, for example, Gottlieb, 1979). Romanes was both a friend and disciple of Darwin's and an evolutionist yet, as discussed below, he was no Darwinist, at least not as we understand the term today. Romanes was, in fact, unable to make much use of Darwin's lasting contributions to the development of evolutionary theory in formulating his own model of the evolution of mind and behavior.

Romanes' phylogeny. If, as Romanes (1882, 1884, 1889) intended in his three major volumes on mental evolution, one is interested in tracing the historical development of mind, intellectual capacity, and behavioral complexity during the history of life on earth, the relationship among extant taxonomic groups should be a major preoccupation. Yet, Romanes was strangely reticent on the question of the phylogenetic relationship among living species. Perhaps he was discomfited by his break with Darwin on the issue; Perhaps he failed to see the contradiction between the view he presented and the one Darwin spelled out with such clarity in *The Origin.* In any case, Romanes touched upon questions of phylogeny only briefly and only in his introduction to *Mental evolution in animals* (1884):

> For throughout the brute creation, from wholly unintelligent animals to the most highly intelligent, we can trace one continuous gradation; so that if we already believe that all specific forms of life have had a derivative origin, we cannot refuse to believe that all the mental faculties which these various forms present must likewise have had a derivative origin. (p. 8)

If the inference to be drawn from this statement is that at some time in the history of the planet there were forms of intermediate intelligence between any two

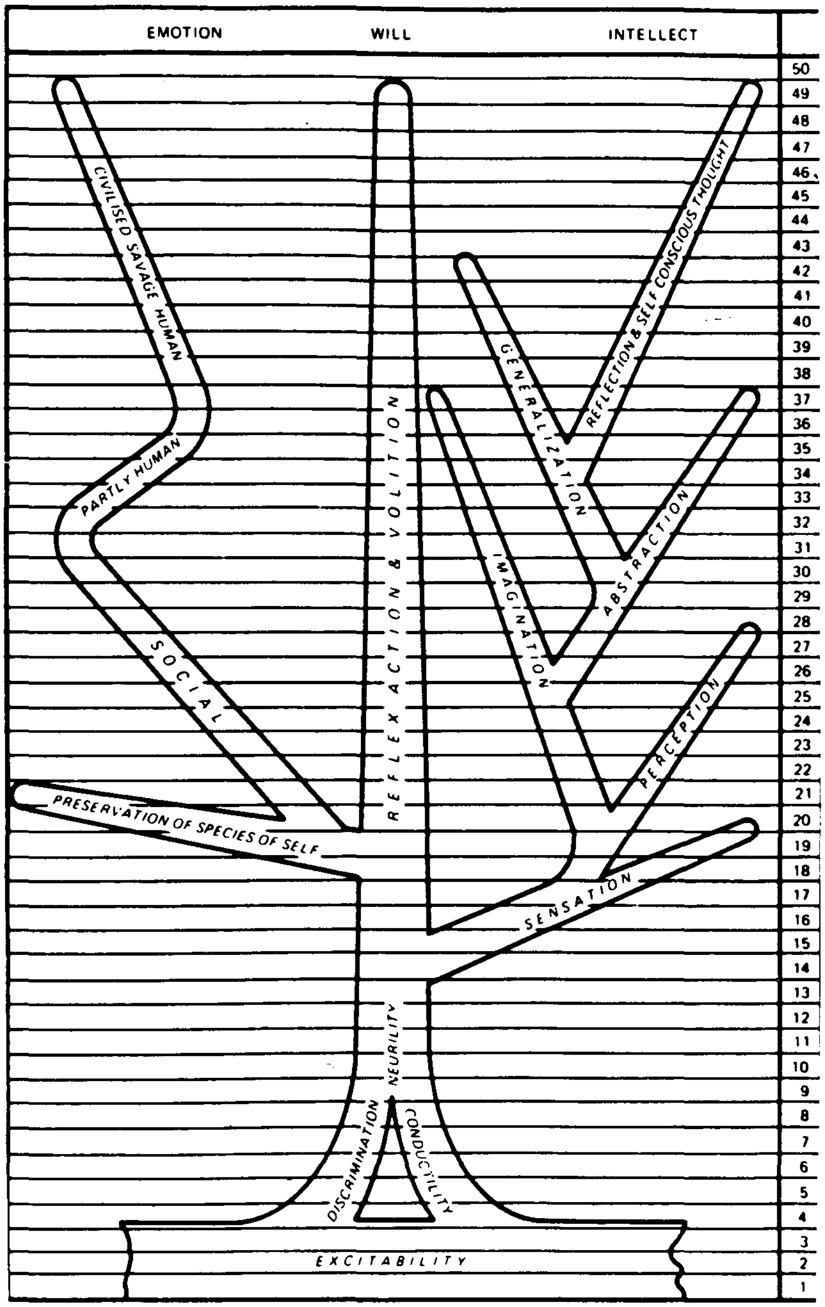

FIGURE 3.1. Romanes' (1884, 1889) tree of mental evolution and "psychological scale," indicating the relative extent of the mental development of different classes of organism.

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PRODUCTS OF EMOTIONAL DEVELOPMENT	THE PSYCHOLOGICAL SCALE	PSYCOGENSIS OF MAN	
			50
			49
			48
			47
			46
			45
			44
			43
			42
			41
			40
			39
			38
			37
			36
			35
			34
			33
			32
			31
			30
			29
Indefinite morality	Anthropoid Apes and Dog	15 months	28
Use of tools	Monkeys and Elephants	12 months	27
Understanding of mechanisms	Carnivora, Rodents and Ruminants	10 months	26
Recognition of Pictures, Understanding of words, Dreaming	Birds	8 months	25
Communication of ideas	Hymenoptera	5 months	24
Recognition of persons	Reptiles, and Cephalopods	4 months	23
Reason	Higher crustacia	14 weeks	22
Association by similarity	Fish and Batrachia	12 weeks	21
Recognition of offspring, Secondary instincts	Insects and Spiders	10 weeks	20
Association by contiguity	Mollusca	7 weeks	19
Primary instincts	Larvae of Insects, Annelida	3 weeks	18
Memory	Echinodermata	1 week	17
Pleasures and pains		Birth	16
	Coelenterata		15
Nervous adjustments			14
			13
	Unknown animals		12
Partly nervous adjustments	probably Coelenterata		11
	perhaps extinct	Embryo	10
			9
			8
Non nervous adjustments	Unicellular organisms		7
			6
			5
			4
Protoplasmic movements	Protoplasmic organisms	Ovum and	3
			2
		Spermtozoa	1

extant species of disparate intelligence in the same historical lineage, then Romanes is simply restating Darwin's position. If to the contrary, the proper interpretation is that we can today trade a continuous gradation of intelligence across extant species, then the proposition remains evolutionary, but is Spencerian rather than Darwinian. The only way to tell what Romanes had in mind is to look at what he did.

The main argument of both *Mental evolution in animals* (1884) and *Mental evolution in man* (1889) is summarized in a single diagram which appears as the frontispiece of both volumes (see Fig. 3.1). Though the diagram incorporates a Darwinian branching tree, the tree bears strange fruit. Its branches are not species, genuses, or families, but an assortment of psychological terms. The relationship among major animal groups is represented not in the tree but in a column to its right labeled "the psychological scale." Here extant groups are linearly ordered from protoplasmic organisms, up through molluscs, insects, fish, reptiles, birds, and rodents to anthropoid apes and dogs. Most revealing, paralleling "the psychological scale" is a list of human ages from embryo to 15 months, the "psycogenesis of man." Each stage in human development is presented as corresponding to a particular level in the taxonomic scale to its left. The diagram is a pictorial representation of Spencer's analogy between ontogenesis and phylogenesis. An historically invalid scale, "the psychological scale," is presented as equivalent to an historically valid one depicting the ontogeny of man. Romanes' view of the relationship among taxonomic groups, while evolutionary, was Spencerian rather than Darwinian.

Romanes on the continuity of animal and human mind. Romanes sought to resolve the question of the role of evolution in the production of the intellectual faculties of man by demonstrating that all mental and moral faculties exhibited by modern man are observable, at least in rudimentary form, in lower animals. Opponents of a continuity of animal and human capacities had stressed the absence of cumulative knowledge in animals and its presence in humans as a fundamental distinction. Thus, one of the most pressing problems for Romanes was to demonstrate the potential for culture in animals.

The first of the tasks Romanes set himself, the accumulation of evidence of rudimentary human-like intellectual and moral traits in animals, proved relatively easy to accomplish. The majority of information available to 19th century scientists interested in the behavior of animals was a great mass of unsystematic descriptions of behavior collected by amateur naturalists. While there were some exceptions, such as Spalding's (1873) elegant experimental work with domestic chickens, most such descriptions were collected by observers studying the behavior of animals from the perspective provided by the Natural Theologians of the preceding century. Creationist scholars like Paley (1802) had proposed that each species was placed on earth by the Almighty either for man's economic benefit or for his moral instruction (Barber, 1980). Such a perspective encouraged the incorporation of anthropomorphic, moralistic glosses into descriptions of the behavior of animals. During the years that Romanes was collecting information on animal behavior, these subjective elements had not yet been purged from descriptions of animal behavior, even those published in the most prestigious journals. Romanes (1884, p. 345), for example, cites a publication in *Nature* by Fitch (1883) on the mental faculties of cats. "Grief is shown by the pining, even unto death upon the removal of a favorite companion; Cruelty by a cat's treatment of a mouse and Benevolence [Mr. Fitch's contribution to the catalogue] by the following instances. . . ." The anthropomorphisms of his correspondents played directly to Romanes theoretical predilections.

Convergence of Romanes' desire to provide evidence of intelligence and morality in animals with the predisposition of his correspondents to find moral lessons in the behavior of animals resulted in Romanes publishing, in 1882, *Animal Intelligence,* a "text-book of the facts of Comparative Psychology" (Romanes, 1882, p. iv) that proved to be a compendium of occasional informative description or experiment, frequent wildly implausible anecdote, and consistent overinterpretation of both.

Romanes' anecdotal methods and anthropomorphisms have been disparaged countless times since Thorndike criticized them in 1898. Romanes (1884) himself recognized that experimental evidence rather than "observing mental phenomena and reasoning from these phenomena deductively" (p. 12) was needed to resolve questions concerning the nature of animal mind. However, Romanes argued that experimental evidence wasn't available and that the question of the origin of human intellect was too important to set aside until appropriate experiments had been conducted.

It is important to recognize that the task Romanes set himself was to find evidence of human-like intellectual and moral traits in animals, believing such evidence necessary to demonstrate the evolutionary continuity of animal and human mind. His constant anthropomorphizing was not the result of carelessness or sloppy thinking. Romanes was, in fact, more cautious than many of his contemporaries in accepting the validity of dubious examples. (See the preface to *Animal Intelligence,* 1882, for criteria of selection of data.) Anthropomorphizing and acceptance of what appear today to be absolutely unbelievable examples of intelligent behavior in animals were required, at least as Romanes saw things, by Darwin's evolutionary theory and the deduction from it of a continuity in the intellectual capacities of man and animals.

THE ORIGINS OF INSTINCT

One of the central problems faced both by Darwin and others of his era was to explain the occurrence of similar complex patterns of adaptive behavior in successive generations of a species. Darwin (1859) offered two theories: First, a thoroughly modern proposal, "Under changed conditions of life, it is at least possible that slight modifications of instinct might be profitable to a species; and if it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable.'' Second, a hypothesis that captured the imagination of many of his contemporaries: ''As modifications of corporeal structures arise from, and are increased by use or habit, and are diminished or lost by disuse, so I do not doubt it has been with instincts.'' Whereas Darwin only reluctantly admitted the nose of the Lamarckian camel under the tent — ''But I believe the effects of habit are in many cases of subordinanate importance to the effects of what might be called spontaneous variations of instinct. . . :'' (p. 209; see also, Darwin, 1871, p. 68), his contemporaries couldn't wait to invite the beast to warm itself by the fire. Eimer (1890) rejected a role for natural selection in the formation of instinct and adopted a purely Lamarckian view. Wundt (1894, p. 389), in discussing theories of instinct, assumed unquestioningly the transmission of acquired characteristics, largely ignored natural selection, and represented that Darwin ''explains instinct as inherited habit.'' Romanes (1884), while adopting Darwin's dual view of the origin of instincts, also put the emphasis on Lamarckian processes:

> Instincts owe their origin and development to one or other of two principles [the first is natural selection]. . . . The second mode of origin is as follows: — By the effects of habit in successive generations, actions which were originally intelligent become as it were stereotyped into permanent instincts. . . . The proof that instincts have had a secondary mode of origin requires to show:
>
> That *intelligent adjustments* when frequently performed by the individual become automatic either to the extent of not requiring conscious thought at all, or as consciously adjustive habits, not requiring the same degree of conscious effort as at first. That automatic actions and conscious habits may be inherited. (p. 180)

In this Romanes is consistent not only with Darwin's but also with Spencer's speculations on the origin of instinct. Spencer had proposed that reflexes and instincts that develop independent of experience in the individual are the consequence of associative learning during the past history of the species.

> Hereditary transmission applies to psychical peculiarities as well as physical peculiarities. While the modified bodily structure produced by new habits of life is bequeathed to future generations, the modified nervous tissues produced by such new habits of life are also bequeathed; and if new habits become permanent, the tendencies become permanent (Spencer, 1855, p. 422).

> Natural selection, or survival of the fittest, is almost exclusively operative throughout the vegetal world and throughout the lower animal world, characterized by relative passivity. But with the ascent to higher types of animals, its effects are

in increasing degrees involved with those produced by inheritance of acquired characters; until in animals of complex structures, inheritance of acquired characters becomes an important, if not the chief cause of evolution (Spencer; 1893, p. 45).

Romanes goes on to argue (1884,) "that instincts may have, as it were, a double root—the principle of selection combining with that of lapsing intelligence [the notion that habitual acts may become instinctive (Lewes, 1860)] to the formation of a joint result" (p. 201). On such a model the variations in behavior on which natural selection acts are not random with respect to their effects on fitness, but are oriented by the learning capacities of organisms. Such a model, predicting oriented heritable variation, also predicts adaptation in the absence of selection: "intelligent adjustment by going hand in hand with natural selection must greatly assist the latter principle in the work of forming instincts, in as much as it supplies to natural selection variations which are not merely fortuitous, but from the first adaptive" (Romanes, 1884, p. 219). Thus, the capacity of animals to learn and to pass on through their gemmules those acquired behavioral traits that enhance survival was, for Romanes, a major driving force in evolution, providing oriented behavioral variation on which natural selection might work. Darwin's Pangenetic hypothesis and tacit acceptance of the possibility of Lamarckian inheritance provided the basis for an alternative to natural selection in the evolution of instincts, an alternative that made the study of learning processes central to the understanding of evolution.

The dual origin theory of instinct proposed by Romanes also provided a mechanism for the accumulation of knowledge by animals, thus obliterating one proposed fundamental distinction between the mental faculties of animals and man. As mentioned previously, supporters of Wallace's contention that there is a difference in kind between human and animal intellectual capacity had pointed to the importance of culture in the life of man and its absence in animals. Romanes (1889) rejected both premises. "I deny on the one hand that mental progress from generation to generation is a peculiarity of human intelligence; and, on the other hand, I deny that such progress is never found to occur in the case of animal intelligence" (p. 13). Through learning, the lapsing of intelligence, and the inheritance of acquired characteristics animals could gradually accumulate extraordinarily complex patterns of instinctive behavior.

To this point, Romanes had added little to models of the development of instinctive behavior proposed by Darwin, Spencer, and Lewes. In fact, Romanes' sole original contribution was to treat as primary a type of learning to which Darwin had assigned a minor role and Wallace (1870) a more important one. Romanes (1884) argued "With animals, as with men, original ideas are not always forthcoming at the time they are wanted, and therefore it is often easier to imitate than to invent" (p. 210). Imitation, primarily of members of one species by another, was for Romanes the main driving force in the evolution of instinct.

Romanes was quick to confess that he could provide almost no evidence of one species of animal imitating the habits of another, but explained away this lack of examples as due to the fact that imitation among species occurred in the past. Today, all one would expect to see is numbers of disparate species with the same instinctive patterns of behavior, though Romanes also failed to provide examples of interspecific communalities in behavior. Clearly, Romanes was not led to his theoretical positions by the weight of evidence. His goal of demonstrating a continuity in the mental life of animals and man, as Darwin had postulated, required, in Romanes' view, demonstration of "mental progress from generation to generation" in animals. It was this requirement that led Romanes, in the absence of evidence, to emphasize lapsed intelligence acting in concert with observational learning to produce adaptive instinctive behaviors. Incorporation of behavioral novelty into a species' instinctive repertoire, following observation of the adaptive behavior of others and the lapsing of intelligence, provided the crucial links between animal and human mind required by theory.

GEMMULES VS. GERM-PLASM 1. AUGUST WEISMANN.

During the years that Romanes was developing his theory of the evolution of instinct, its foundations in Darwin's theory of Pangenesis were already under attack. In 1883, August Weismann, a cytologist and developmental biologist, rejected the notion of inheritance of acquired characteristics. Weismann undertook to demonstrate experimentally that the structure and division of cells is such as to make an inheritance of acquired characteristics impossible. He argued that germ cells segregate early in development and, in consequence, there was no way in which influences acting on the remainder of the organism could be transmitted to the nuclei of germ cells in which heritable information resides. Weismann's attack (1883, in Weismann, 1889) on Romanes' view of the evolution of instinctive behavior was both clear and direct:

> It is usually considered that the origin and variation of instincts are also dependent upon the exercise of certain groups of muscles during a single life time; and that the gradual improvement which is thus created by practice is accumulated by hereditary transmission. I believe that this is an erroneous view, and I hold that all instinct is entirely due to the operation of natural selection, and has its foundation, not upon inherited experiences, but upon variation of the germ. (p. 91)

As Romanes (1893) stated in a book he wrote in spirited defense of Darwin's theory of Pangenesis against Weismann's germ-plasm theory, "The theory of germ plasm is not only a theory of heredity, it is also, and more distinctively, a theory of evolution" (p. 103). While Darwin's theory of gemmules allowed

Lamarckian processes, the theory of germ-plasm excluded them as physiologically impossible. If Weismann were correct, learned behavior could not become hereditary, learning played no role in the evolution of instincts, all of Romanes' elaborate demonstrations of "mental progress from generation to generation" were false, and much of his evidence of continuity in animal and human faculties was untenable.

To the behaviorist, the critical question became whether the behavioral phenomena Romanes had claimed demonstrated inheritance of acquired characteristics could be explained in other ways (Spencer, 1893).

GEMMULES VS. GERM-PLASM 2: C. L. MORGAN

Morgan's four major texts on animal behavior (1890, 1894, 1896, 1900) are each, in part, concerned with the question of the role of learning in the evolution of instincts, the behavioral version of the gemmule-germ plasm controversy. In *Animal Life and Intelligence,* Morgan (1890) recognized three factors in the origin of instinctive activities: elimination through natural selection, selection through preferential mating [Darwin's (1871) notion of sexual selection] and inheritance of individually acquired modification. These he ranked, as to their respective likelihood, as incontrovertible, highly probable, and "probable in a less degree" (p. 447). Yet, following Romanes, Morgan suggests that intelligence may have been a factor in all three paths for the development of instincts. For example, "Some of the habits which survived elimination under [natural selection] may have been originally intelligent, some of them from the first unintelligent" (Morgan, 1890, p. 447). At this point in Morgan's thinking he had no doubt that the intelligent adjustments of behavior exhibited by organisms provide at least some of the variability on which both natural and sexual selection act. Like Romanes and Wallace, Morgan also attributed considerable importance to imitative learning and the tuition of young by their parents, though Morgan treated these types of learning as basically conservative, acting to preserve already established behaviors, and only rarely encouraging the spread of novel habits.

In 1896, Morgan began to express serious doubts about the possibility of the lapsing of intelligence and inheritance of acquired characteristics. Observations that in 1890 were fairly compelling evidence of transmission of acquired behavior were, in 1896, treated far more circumspectly. He came to the realization that even the anecdotal evidence of hereditary transmission of learned behaviors was "surprisingly small in amount" (Morgan, 1896, p. 294) and open to alternative interpretation. In *Habit and Instinct* (1896) Morgan suggests that experimental rather than observational data are needed to resolve the issue. After some 25 pages of discussion he reaches the conclusion, quite contrary to the one he held in 1890, that "there is but little satisfactory and convincing evidence in favour of [hereditary] transmission [of acquired traits]'' (1896, p. 305). The previous 45 years of research and theorizing on the role of learning in the evolution of heritable behaviors was finally called into serious question. The growing acceptance by biologists of Weismann's view of the separation of germ cells and somatic cells early in development and the consequent conclusion that the direct transmission of acquired characteristics, whether somatic or behavioral, is impossible, had finally undermined the research program Romanes had undertaken in Darwin's name. However, as Morgan was to make clear, rejection of Lamarckian arguments did not logically preclude an important role of learning in evolutionary process and in the evolution of instinct. Morgan remained convinced that ''variation does seem in some cases to have followed the lines of adaptive modification, so as to suggest some sort of connection between them'' (1896, p. 305). He proposed a novel theory, integrating learning and natural selection, to explain the proposed connection.

In one of those striking coincidences of intellectual history, three scientists, J. Mark Baldwin (1896), H. F. Osborn (in Dyar, 1896) and C. Lloyd Morgan (1896) each put forward independently, and at nearly the same time, a theory to explain how the learned behavior of organisms might, in the absence of Lamarckian transmission, guide both the course of evolution and the evolution of instinct. C. L. Morgan's (1896) statement of the argument is, to the modern reader at least, the clearest of the three. He asks his reader to imagine a species, capable of learning, whose members face a novel environmental challenge. Morgan proposes, first, that those individuals with greater inherent capacity to modify their behavior to meet the new circumstances would be more likely to survive and reproduce. Further, Morgan suggests, any congenital variation that enhanced the probability of acquisition of the learned modification would be selected for, and any congenital variation which reduced its probability of acquisition would be selected against. Over evolutionary time, the result of such a process would be an increase in the predisposition of members of the species to acquire the adaptive modification of behavior necessary to meet the new challenge. Eventually, a pattern of behavior, originally dependent on individual plasticity for its development, might be expressed in the absence of experiences once necessary for its development. Thus, ''plastic modification leads, and germinal variation follows'' (Morgan, 1896, p. 320).

Morgan concludes his discussion of his theory with the statement,

> . . . we may, in the face of the biological difficulties which render direct transmission more and more hard to accept, adopt some such view as the foregoing, and while still believing that there is some connection between habit and instinct, admit that the connection is indirect and permissive rather than direct and transmissive. (p. 322)

The Morgan-Baldwin-Osborne hypothesis was well received both by contemporaries (e.g., Holmes, 1911) and future biologists (e.g., Mayr, 1976). It might have served as a new focus for the study of the relationship between learning and evolution. For Thorndike, however, it was clearly too little too late. Thorndike's failure to cite Darwin or mention evolution in his 1898 monograph was no simple oversight. He viewed the work of his predecessors, studying learning within an evolutionary framework, as unmitigated failure. Darwin's use of anecdotal evidence provided by correspondents, so effective in unravelling the mysteries of organic evolution, had produced little but confusion in the study of behavior. Thorndike sought to replace such anecdotalism with controlled experiment. Two score years of studying animal learning within an evolutionary perspective had proved futile. Thorndike rejected evolutionary discussion, advocating in its stead careful analyses of learning mechanisms of the sort Morgan had suggested, but seldom employed, in his *Introduction to Comparative Psychology* (1894). Thorndike's research on learning by imitation in animals, a process Spencer, Wallace, Darwin, Romanes, and Morgan had emphasized to varying degree in attempting to exemplify the continuity of mind from animal to man, and his failure to find evidence of such learning in cats, dogs, chickens, and monkeys, broke the major empirical link with the past. The further failure of a series of similar research projects using as subjects birds (Porter, 1910) raccoons (Cole, 1907; Davis, 1907), rats (Berry, 1906; Small, 1899), cats (Berry, 1908), and various primates (Hobhouse, 1901; Kinnaman, 1902; Haggerty, 1909; Watson, 1908) to provide convincing evidence of imitative learning (Holmes, 1911; Washburn, 1908) further discredited the approach of earlier students of animal learning. The study of animal learning was to begin anew with the work of Thorndike on the laws of effect and exercise.

It would have been satisfying to be able to end this chapter where I started, with Thorndike's (1898) rejection of evolutionary theories in the study of learning. The facts are not quite so simple. In an expanded version of the 1898 monograph, published in 1911, Thorndike devoted his final chapter to the question that had motivated Romanes' work on animal intelligence, that of the continuity of animal and human mind. Thorndike's solution is uninteresting. It is largely that proposed more than 60 years earlier by Spencer, "the intellectual evolution of the race consists in an increase in the number, delicacy, complexity, permanence and speed of formation of . . . associations. In man this increase reaches such a point that an apparently new type of mind results, which conceals the real continuity of the process" (Thorndike, 1911, p. 294). It was a view with which Spencer and Romanes, but not Darwin, would have been comfortable, a view that would be incorporated into the work of comparative psychologists of succeeding decades. The notion of a gradual linear increase in complexity of brain, resulting in corresponding increasing complexity of learning, is evolutionary in the broadest sense, but fails to make contact with evolutionary theory as it was understood even at the turn of the century. Thorndike, while embracing the notion of an evolution of associative capacities, abandoned the attempt to employ particular theories of evolutionary process as a tool in the study of the mechanisms of learning. It is only during the past 2 decades that the enterprise initiated by Darwin has again captured the attention of the psychological community.

CONCLUSIONS

The first attempts to integrate the study of animal learning and evolutionary theory failed in large measure because the evolutionary theory adopted by those interested in the evolution of mind and behavior was later shown to be false. It is easy to argue that this failure provides no lesson for those who are today interested in the interaction of learning and evolution. Perhaps our evolutionary models are basically correct and will not lead us into error. However, the lapses apparent in the work of many of the outstanding behaviorists of the nineteenth century do provide a warning that should be heeded regardless of the truth or falsity of our current view of evolution. That warning concerns the relationship between evolutionary theory and the interpretation of behavioral data.

Convincing evidence of both learning by observation and the inheritance of acquired characteristics was reported by almost all 19th-century students of behavior from Darwin to Morgan. By the turn of the century, few saw compelling evidence of either.

Animals have a surprising tendency to behave in accord with the hypotheses of those who observe them. It is difficult to avoid finding those capacities in animals that evolutionary theory suggests they should possess. We should not forget, as 19th-century students of behavior largely did, that natural selection is constrained by limitations imposed by the variations occurring in natural populations. Surely, natural selection would have produced a mechanism for the inheritance of acquired characteristics if the biochemical process for the translation of DNA into protein did not forbid it. Equally surely, natural selection would have produced a robust capacity for observational learning in animals, if as yet poorly understood constraints on the evolution of associative processes did not stand in the way.

Evolutionary theory may prove a useful heuristic in the search for adaptive associative capacities in animals, but the probable adaptive value of a capacity, if it were to evolve, is not evidence of its actual evolution. Overenthusiasm for predictions deduced from logically consistent theory is as rich in potential for error in 1985 as in 1885. There are limitations on the adaptive potential of organisms, phylogenetic or ontogenetic constraints on the directions in which evolution can proceed. Deductions from evolutionary models are not facts, but working hypotheses, requiring rigorous experimental test. The failure to appreciate the distinction between prediction and evidence, so clearly evident in the first attempts to integrate the study of animal learning and evolution, can serve as a caveat for today.