The International Journal of Comparative Psychology, Vol. 2, No. 3, Spring 1989

WHAT SHOULD COMPARATIVE PSYCHOLOGY COMPARE?

N. K. Innis
J. E. R. Staddon

University of Western Ontario and Duke University

ABSTRACT: Scientific psychology is a search for the mechanisms that underlie behavior. Following a brief history of the comparative psychology of learning, we suggest that comparative psychologists should focus on mechanisms rather than performances, and provide an example of a simple, formal mechanism to illustrate this point.

The modern history of comparative psychology begins with Charles Darwin (1809-1882). Darwin's theory of evolution through variation and natural selection has provided a conceptual framework for psychology as well as for biology. As Tooby and Cosmides (p. 175) point out, the two parts to Darwinian evolution have led to two kinds of approach to the study of animal behavior: an emphasis on variation underlies the phylogenetic approach; an emphasis on natural selection underlies the study of adaptation. In this introductory paper we consider the comparative psychology of *learning*, perhaps the most complex behavioral adaptation and the topic most popular with psychologists. After a brief overview of some historical highlights, we focus on the issue of comparison. What have comparative students of animal learning chosen to compare? Has their work been successful? What should be compared?

HISTORICAL BACKGROUND

Several recent volumes (e.g., Boakes, 1984; Dewsbury, 1984; Richards, 1987) examine in detail the history of comparative psychology and Darwin's influence on it; we mention only a few of the more important early contributions. Following the publication of *The Descent of Man*

Address correspondence to either author at the Department of Psychology, Duke University, Durham, NC 27706.

(1871) and *The Expression of the Emotions in Man and Animals* (1872), in which Darwin's ideas concerning the evolution of intelligence were presented in some detail, naturalists became interested in studying the animal mind. One of the first to write extensively on the topic was George Romanes (1848–1894), a friend and champion of Darwin. As Romanes (1882) indicated in the Preface to *Animal Intelligence*, his aim was to offer a scientific textbook of comparative psychology that provided both facts about the levels of intelligence attained by various species, and a consideration of animal intelligence in terms of Darwinian theory. While Romanes' intentions were scientific, his reliance on anecdotes soon drew severe criticism, particularly from C. Lloyd Morgan (1852–1936). It was not long before Morgan (1894), in his own textbook *An Introduction to Comparative Psychology*, established one of the standards for future work in comparative psychology. In what came to be known as Morgan's Canon, he warned against anthropomorphic explanations, recommending that care should be taken not to interpret an action as the result of a higher mental process if, in fact, it could be explained by one at a "lower level in the psychological scale" (p. 53). Nevertheless, despite Lloyd Morgan's strictures, most comparative psychologists believed they were comparing faculties or abilities—not just phenomena or activities, and certainly not processes, in the modern sense.

The textbooks of comparative psychology at this time were in the tradition of contemporary works in comparative biology and anatomy. Chapters considered, in turn, examples of the behavior of a large number of species of various degrees of complexity and relatedness, on a variety of tasks. The emphasis then was on identifying and examining similarities and differences in capability and intelligence across animal species. The most influential textbook of this type in North America during the early years of the twentieth century was Margaret Washburn's *The Animal Mind* (1908), which was to remain popular through several subsequent editions. But this tradition was not to persist: While there would always be some biologically oriented students of animal behavior who maintained a concern with phyletic differences, the stream of psychology was soon to be diverted by a different current.

American Functionalism—Mind Surrenders to Behavior

A new theoretical force—Behaviorism—emerged early in the twentieth century. Although eventually it was to radiate into many varieties, from radical to purposive, Behaviorism from the outset altered the approach taken by comparative psychologists. Behaviorism was the offspring of the functional movement that was gaining ascendance in North America at this time, particularly at places like Chicago and Columbia. Since the predominant aim of the functionalists was to ameliorate the human condition, it is not surprising that they found the adaptive function of behavior more intriguing than its evolutionary origins, and situational factors more significant than hereditary predispositions. As this new wave of environmentalist thinking took hold, boosted by the polemical efforts of John B. Watson (1878-1958), the "father"—or at least the publicist—of Behaviorism, evolutionary theory provided the justification for studying animal behavior as the precursor of the behavior of human beings. But evolution was otherwise largely ignored.

As the name Behaviorism implies, animal mind was displaced by animal action. Most experimental psychologists began to study the ways in which animal behavior was altered by environmental experience—animal learning. Two basic approaches to learning, initially ill-distinguished, soon began to shape the study of animal behavior, as Pavlovian conditioning and Thorndike's Law of Effect became the central paradigms guiding animal research. With these developments, researchers soon shifted away from studying a wide range of species, looking instead at the details of learned responding in a small, but presumably representative, set. The fields of comparative and animal psychology to a large extent were subsumed by learning theory. This change is exemplified by the emphasis placed on animal learning in one of the most popular texts, Moss's (1934) *Comparative Psychology,* a book that was widely used through three editions over the next 25 years. There were, of course, exceptions to these general trends, particularly in the work of Schneirla and his associates (see, for example, Maier & Schneirla, 1935/1964), and there is some room for difference of opinion about the dominance or otherwise of learning theory during this period (cf. Dewsbury, 1984; Innis, 1987).

Nevertheless, it seems fair to summarize the recent history of comparative psychology in terms of the shift from a concern with phylogeny to a predominant interest in learning and the effects of experience. Following Darwin, students of animal intelligence attempted to identify the intellectual capacities of various animal species and to categorize them in ways that might say something about the evolutionary history of the species and the capacity studied. This phyletic approach was purely descriptive and initially involved primarily anecdotal evidence, although later more scientific field studies were carried out. A major change in approach occurred, particularly in North America, as the functionalist, and later behaviorist, schools of psychology began to predominate. Animals now became tools, in contrived laboratory settings, with which to examine a small set of general rules proposed by learning theorists. These rules concerned the ways in which behavior changes as the result of experience and were of interest primarily for what they could teach us of ways to improve human life. The focus shifted away from phyletic comparison towards the prediction and control of action, with clues to better technique to be provided by limited cross-species comparison.

The Comparative Psychology of Learning

It was not just that psychologists turned to the study of animals to explain the behavior of humans. They also accepted, often without much discussion—at least during the early years—the idea that associative learning is a primitive property, a basic element of the vertebrate *bauplan*, like quadrupedalism or the circulatory system. Regarded from this point of view, the differences between ape and reptile—and man—could be seen as mere parameter adjustments and complexifications of the same basic general learning process. This general process assumption allowed animal psychologists to focus on a small set of representative species—monkeys, pigeons, but primarily the white rat—for which experimental procedures had been well-tested and whose maintenance conditions were well-known.

In an attempt to provide a fresh agenda for comparative psychology M. E. Bitterman (1960; 1975), a Schneirla student in his undergraduate days, suggested a new, more sophisticated goal: Rather than looking just at the ability of different species to perform adequately on supposedly comparable tasks—an almost impossible constraint, given vast and hard-to-quantify differences in motivation and sensory, motor and perceptual abilities among species—comparative psychologists should be comparing the functional relationships displayed by different species under roughly analogous learning conditions. For example, while we cannot reasonably expect a goldfish to press a target as fast or as forcefully as a rat, perhaps the relation between (say) rate of pressing and reward rate will be similar in both species.

Bitterman concentrated on data for five "prototype" species (goldfish, turtle, pigeon, rat and monkey), examining a number of learning phenomena that had been extensively studied in rats: reversal learning, probability matching, partial reinforcement effect, reinforcement contrast effects, and several others. He reported numerous similarities across species, and also a few notable differences. For example, he claimed that fish and rats differ in the processes underlying both serial reversal and probability learning. Pigeons he found to be rat-like (they improved) on serial reversal, but fishlike (they matched rather than maximized) on some probability learning tasks (Bitterman, 1965). His conclusion that these empirical differences between a "lower" and a "higher" species must reflect the progressive evolution of new mechanisms did not go unchallenged, however. Mackintosh (1969; Bitterman & Mackintosh, 1969), while not questioning the differences in performance, took issue with the inference that different underlying processes are involved. Mackintosh maintained that the behavioral differences may be merely quantitative and could be accounted for by a single mechanism, "say, some differences between the parameters used to explain the behavior of rats and those used for the fish . . ." (1969, p.

138), a position identified particularly with the earlier work of C. L. Hull (e.g., 1943). Unfortunately, Mackintosh made no concrete suggestions along these lines, referring instead to an attentional hypothesis that he himself characterized as "vague," which was not convincing to Bitterman. Thus, the one- vs. two- process dispute remained unresolved.

The apotheosis of the one- process view is the recent work of Macphail (1982; 1987) who has argued (somewhat extravagantly) for the essential identity of all nonlinguistic learning across the whole vertebrate phylum—although his arguments still lack the kind of quantitative theoretical basis identified as ideal by Hull and Mackintosh.

Research along the lines proposed by Bitterman has focused recent attention on the question of learning processes. Nevertheless, the fact that Macphail (1987) can seriously argue for the essential identity of all nonlinguistic intelligence, and elicit a mass of respectful if largely critical commentary, shows we still lack deep understanding of the processes involved in associative learning. Despite the efforts of Bitterman, Mackintosh and a few others, the experimental comparative focus is still very much on phenomena rather than mechanisms. Perhaps it is time to put some flesh on the suggestion that many, perhaps all, differences among species can be accounted for by "mere" parameter variation of a single, or at most a small number, of "basic processes."

MECHANISMS OF ANIMAL LEARNING

Our thesis, which we will illustrate by example, is that assertions about the essential identity, or lack thereof, of any faculty or process across species are vacuous in the absence of fairly detailed specification of the mechanisms involved. The papers by Bitterman and Mackintosh in which this issue first came to the fore are now quite old, but process equivalence is far from a dead issue in psychology. It is a hot topic in memory research for example, where vigorous debate surrounds the question of multiple memory systems: How many are there, and what are their properties (e.g., Tulving, 1985; Sherry & Schacter, 1987)? In comparative psychology, Macphail's (1982; 1987) provocative thesis has fueled recent controversy about the essential unity or diversity of all infrahuman intelligence. Bitterman, for example, has taken strong issue with Macphail's evaluation of the *successive negative contrast effect* (SNCE), i.e., the slower or less accurate responding of animals trained with a small reward following training with a larger reward, compared with the performance of animals trained from the outset with a small reward. Goldfish generally fail to show this effect, which is easily demonstrated in rats and several other animals and birds. On this basis, Bitterman concludes that goldfish are lacking some mechanism that evolved later on: ". . . the mechanism of successive negative contrast (whatever it may be) evolved in some common reptilian ancestor of birds and mammals (Bitterman, 1987, p. 659)." Macphail, on the contrary, argues that the failure to find the SNCE in goldfish is not decisive disproof for his unitarian position.

We believe that this argument—indeed, all such arguments—cannot be resolved without putting in play some specific theory, either for two processes (Bitterman's position) or one (Macphail's position). We will try to illustrate our point by example. We hope we can persuade comparative psychologists to relinquish fruitless and inconclusive debates of the "one mechanism or two" variety, and concentrate instead on proposing and testing specific, detailed mechanisms for the phenomena in which they are interested.

Habituation and Sensitization: A Simple Model System

We are not yet in a position to offer the kind of theory of the SNCE that would satisfy Mackintosh's criterion. But it is possible to speculate in a relatively straightforward way on mechanisms for the much simpler phenomena of habituation and sensitization. Our aim is not so much to provide a definitive theory as to make a methodological point using these elementary adaptive phenomena as an example.

Habituation is the waning in strength of response, such as the startle response, to repeated stimulation. Sensitization is an increase in the strength of a response as a stimulus is presented repeatedly. Figure 1

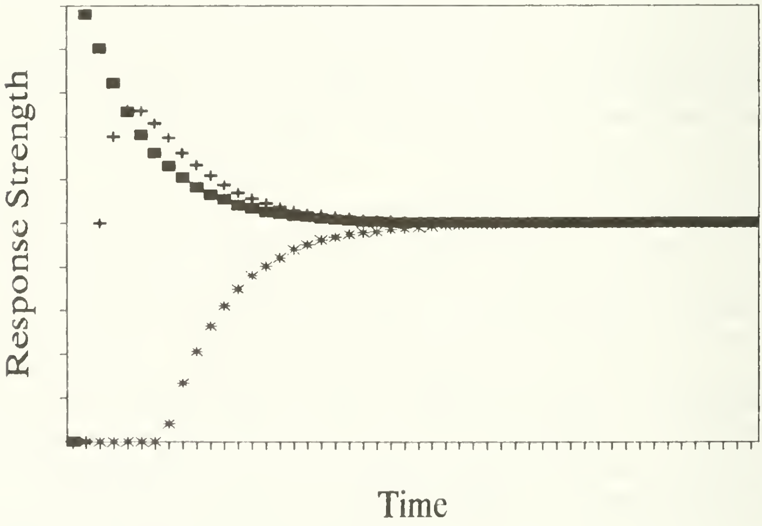

FIGURE 1. Response of three hypothetical "species" to repeated stimulation. Species A (filled squares) shows habituation; species B (stars) shows temporal summation and sensitization; species C (crosses) shows a biphasic response. Parameter a is a time constant: values for each species are given. See text.

shows three sets of imaginary data from habituation/sensitization experiments with stimuli of comparable affective tone. The three graphs show response strength, of three species, to a series of repeated stimuli. Species A (filled squares) shows clear evidence for habituation: response strength decreases across the series. Species B (stars) shows temporal summation and then sensitization: initial stimulus presentations have no effect, but then response strength increases across the series. Species C (crosses) shows a biphasic effect: at first there is sensitization—response strength increases—but then there is habituation (response strength declines from its maximum value early in the series).

The question: Can we tell from these data whether there is a single underlying process across all three species, or two processes, or several? Obviously we would want to do more experiments before committing ourselves. Figure 2 shows the results of one such experiment, in which we have varied intertrial interval, which was one time unit in Figure 1, and is two units in Figure 2. Now we see larger differences among the three species. Species A still shows habituation, species B sensitization and species C a biphasic effect, but the absolute levels of the responses now differ substantially among the three species: species A consistently shows the highest level of responding, B the lowest and C is intermediate. Moreover, species A's steady-state response has increased, but the steady-state response of the other two species has decreased, an informative dissociation, one might think. Evidently trial spacing affects the absolute level but not the general form of the response vs. trials function.

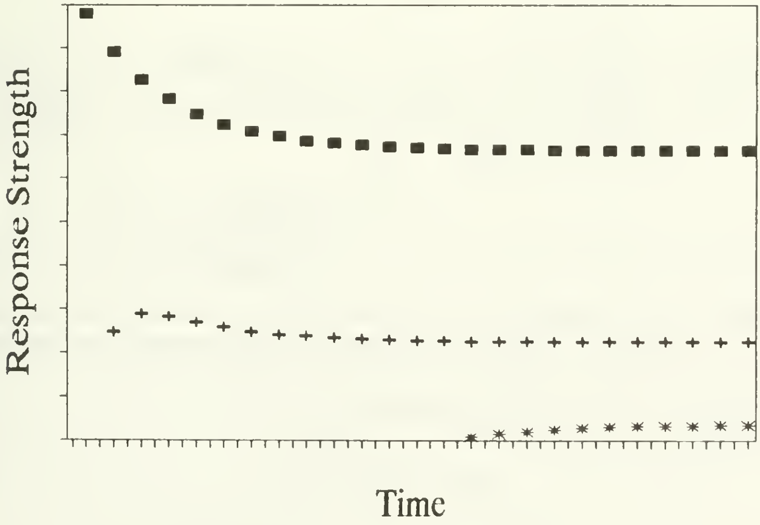

FIGURE 2. Response of three hypothetical species to repeated stimulation at an interstimulus interval twice that in Figure 1. Species A; filled squares; species B: stars; species C; crosses. Parameter a, as in Figure 1.

Given this kind of stability of pattern differences, but divergences in direction of change under experimental manipulation, many would feel safe in concluding that here we do indeed have at least two and perhaps three different processes: Species A (a fish, perhaps) shows process 1 (habituation), species B (reptile?) process 2 (sensitization), and species 3, which is clearly more advanced (mammal?), both processes.

Figure 3 shows the process that actually generated all the curves in the first two figures. It is a single process, by definition, but it does have several identifiable components: two integrators, a comparator and a threshold. Each integrator is a "leaky bucket" process that can be described by a simple discrete-time linear operator. Thus, for integrator 1 (which is responsible for both temporal summation and sensitization):

$$Ve(t+1) = aVe(t) + (1-a)\,X(t) \qquad (1)$$

where $Ve(t+1)$ is the output of the system at time $t+1$, $X(t)$ the stimulus input at time t, and a is a time constant: the higher the a value, the smaller the effect of the current input compared to past inputs, i.e., the longer the time period over which temporal summation can occur. A similar equation describes the second integrator (which accounts for habituation).

$$Vi(t+1) = bVi(t) + (1-b)Vo(t) \qquad (2)$$

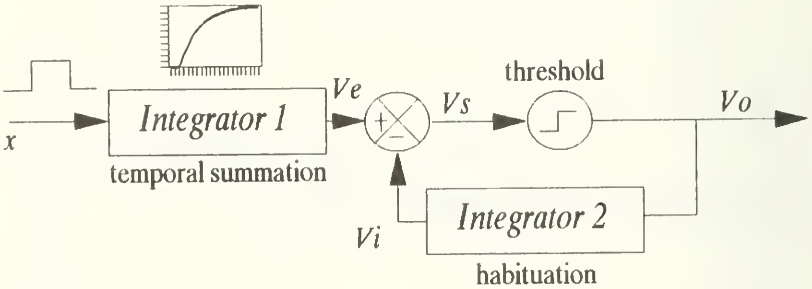

FIGURE 3. System of two integrators and a threshold that produced the data shown in Figures 1 and 2. Parameter values: a = 0.01 (species A), 0.9 (species B), 0.5 (species C); b = .09 and θ = 0.5 for all three species. See equations in text.

Two additional equations complete the picture

$$Vs(t) = Ve(t) - Vi(t) \qquad (3)$$

$$Vo(t) = V_S(t) - \theta, \text{ if } V_S > \theta, 0 \text{ otherwise} \qquad (4)$$

Thus, the system is completely described by four equations with three free parameters: two times constants, *a* and *b*, and a threshold, θ. Equations 1 and 2 are integrators; Eq. 3 describes how *Ve* (the excitatory effect of the stimulus) and *Vi* (the inhibitory effect of the response—a good Hullian concept) combine to produce the "action potential," *Vs*. Equation 4 describes how action potential, *Vs*, is "thresholded" to produce response amplitude, *Vo*.

The relation among the three main variables in the system, *Ve*, *Vi*, and *Vs*, and the input, *X*, is shown graphically in Fig. 4.

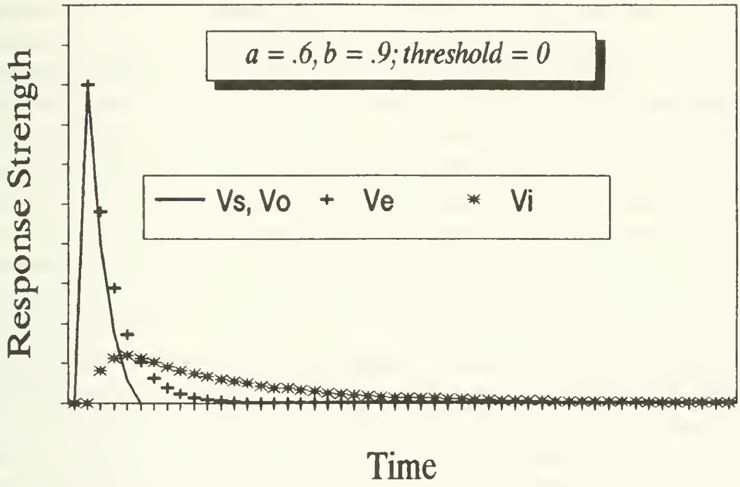

FIGURE 4. Response of the components of the system shown in Figure 3 and equations 1-4 in the text to a single stimulus presented at t = 0. The threshold parameter, θ, is set to zero; time constant $a = 0.6$, time constant $b = 0.9$. Solid line: system output ($V_S = V_eV_i, = V_O$, for $\theta = 0$); crosses: exitatory response (first integrator: V_e); stars: inhibitory response (second integrator: V_i).

Thus, despite the apparent differences among our three species, a relatively simple process, determined by just three parameters, is sufficient to generate all of them. Moreover, the differences among species reflect variation in just one of the three parameters, *a*, the time-constant for the excitatory (sensitization) component. We can also say that the system described in Eqs. 1-4 is close to the minimal system, in the sense that an asymmetrical biphasic response pattern, the most complex pattern in the data, requires at least two parameters for its specification. But of course there are very many other two- or three-parameter systems that might be adequate to account for this limited data set.

To validate this or any other black-box model, two further steps are necessary. First, test experimental predictions: a real-time dynamic model like this is very powerful, in the sense that it makes exact predictions about the pattern of response amplitude to any pattern of input stimuli. It is therefore exceedingly easy to disconfirm (perhaps this is why so few such models survive). Second, if the model withstands all experimental tests, it becomes worthwhile to look beyond the *formal* mechanism to the actual *physiological* processes that must carry out the formal operations (cf. Fentress, 1980). Can we find measurable physiological processes (transmitter uptake rates, creation or dissolution of ionic channels, neuroanatomical constraints, etc.) corresponding to the structure and parameters of the model? This second step is more likely to be successful the better the model judged purely on the basis of black-box experiments. Moreover, step 1 need not be absolutely complete before embarking on step 2. Once the main outlines of the formal process are clear, it may well be more efficient to refine the details by looking closely at the neurophysiological underpinnings—than by further black-box elaborations. No one can provide a recipe for the optimal research strategy; each problem must obviously be judged on its own merits and in light of the information and research opportunities available at each level, blackbox or physiological.

What is the role of between-species comparison in this endeavor? We believe that variation in species is not different—in its role as part of a research strategy—from variation in any other experimental condition, such as motivational type and level, stimulus intensity and quality, stimulus sequence, etc. We know something, *a priori*, about each of these things. Stronger stimuli we know will generally elicit larger responses from the appropriate sensory receptor and will be subject in their effects to psychological constraints such as Weber-law effects. Similarly, different species stand in more or less well-known phylogenetic relationship to each other. Species A may be closer in its morphology to the common ancestor of species A, B and C than either B or C; thus we may expect that many of the features of B and C represent identifiable transformations (according to the kinds of developmental rules discussed by Gould, 1977, for example) of homologous features in C. Although there are no set rules for comparison, these phylogenetic relationships impose constraints that may limit the search for possible mechanisms to sets that by simple transformation or parameter adjustment can encompass the behavior of all three species. Thus, following the only true scientific method—of guesswork, donkeywork, prediction and test—between species comparisons can aid the search for understanding of behavior, brain, and the relations between the two.

CONCLUSION

Scientific psychology is a search for the mechanisms that underlie behavior. Every scholarly field, as part of its dynamic of self-preservation, tends to be both imperialistic and exclusionary (Staddon, 1987). Thus, we have economists seeking to explain biology or psychology in economic terms, literary "deconstructionists" arguing that scientific theories are neither true nor false but merely "texts" as subject to their interpretation as *Fanny Hill* or *The Scarlet Letter* (see Crews, 1986, for a critical account)—and psychologists asserting that there are laws of individual behavior that transcend, or at least cannot be reduced to, physiology. While this view may ultimately be borne out, we see little reason to accept it on present evidence. The best worked out psychological laws, of color vision or psychophysics, for example, have always turned out to relate very directly to the neural machinery involved.

From this point of view, between-species comparison is just one of a number of tools we can use to understand mechanism—formal or, ultimately, physiological—and as we have tried to show, many comparative psychologists, such as Mackintosh and Bitterman, have so viewed it. Like any tool, its value is to be judged by its effectiveness: How helpful is it to our understanding of learning mechanisms (for example) to compare the learning of goldfish, rat and pigeon? Since we still know rather little about the learning mechanisms of any species, this question is still open—although few would doubt the value of looking at more than one species.

We have argued that there are important limitations on what can be inferred from comparing learning performance across species: Different performance patterns cannot be taken as evidence for different underlying mechanisms. And, symmetrically, similar performance cannot be taken as evidence for similar mechanisms (the monotonic 2-parameter curves in Fig. 1 and 2 could easily be modeled by a process with one parameter plus a constant base rate, for example). These limitations are in fact quite well known to most thoughtful theorists (cf. Elepfandt, 1987). Nevertheless, the obvious implication is widely ignored: To argue for one, two, or many learning processes in the abstract, without specifying what these processes actually are—at a level where they can be subjected to the kind of searching test we illustrated with our habituation model—is to embark on a debate without any possibility of resolution.

ACKNOWLEDGEMENTS

We thank M. E. Bitterman for comments on an earlier version that did not quite cause us to abandon the work entirely. Thanks also to N. J. Mackintosh. NKI thanks the Canadian SSHRC and JERS is grateful for research support from the NSF.

REFERENCES

Bitterman, M. E. (1960). Toward a comparative psychology of learning. *American Psychologist, 15,* 704-712.

Bitterman, M. E. (1965). Phyletic differences in learning. *American Psychologist, 20,* 396-412.

Bitterman, M. E. (1975). The comparative analysis of learning: are the laws of learning the same in all animals? *Science, 188,* 699-709.

Bitterman, M. E. (1987). Evidence of divergence in vertebrate Learning. *Behavioral and Brain Sciences, 10,* 659-660.

Bitterman, M. E. & Mackintosh, N. J. (1969). Habit-reversal and probability learning: Rats, birds and fish. In R. M. Gilbert & N. S. Sutherland (Eds.) *Animal discrimination learning.* New York: Academic Press.

Boakes, R. A. (1984). *From Darwin to Behaviourism: Psychology and the minds of animals.* Cambridge: Cambridge University Press.

Crews, F. (1986). *Skeptical engagements.* New York: Oxford University Press.

Darwin, C. (1871). *The descent of man and selection in relation to sex.* London: J. Murray.

Darwin, C. (1872). *The expression of the emotions in man and animals.* London: J. Murray.

Dewsbury, D. A. (1984). *Comparative psychology in the twentieth century.* Stroudsburg, PA: Hutchinson Ross.

Elepfandt, A. (1987). Comparative cognition: Inadequate approach, precipitate conclusions. *Behavioral and Brain Sciences, 10,* 661-662.

Fentress, J. C. (1980). How can behavior be studied from a neuroethological perspective? In H. M. Pinsker & D. W. Willis, Jr. (Eds.) *Information processing in the nervous system.* New York: Raven Press.

Gould, S. J. (1977). *Ontogeny and phylogeny.* Cambridge, MA: Belkap Press.

Hull, C. L. (1943) *Principles of behavior: An introduction to behavior theory.* New York: Appleton-Century.

Innis, N. K. (1987). Edward C. Tolman: Comparative psychologist? In E. Tobach (Ed.) *Historical perspectives and the international status of comparative psychology.* Hillsdale, NJ: Erlbaum.

Mackintosh, N. J. (1969). Comparative studies of reversal and probability learning. In R. M. Gilbert & N. S. Sutherland (Eds.) *Animal discrimination learning.* New York: Academic Press.

Macphail, E. M. (1982). *Brain and intelligence in vertebrates.* Oxford: Clarendon Press.

Macphail, E. M. (1987). The comparative psychology of intelligence. *Behavioral and Brain Sciences, 10,* 645-695.

Maier, N. R. F. & Schneirla, T. C. (1935/1964) *Principles of animal psychology,* Enlarged Edition. New York: Dover.

Morgan, C. L. (1894). *An introduction to comparative psychology,* London: Walter Scott.

Moss, F. A. (Ed.). (1934). *Comparative psychology.* New York: Prentice-Hall.

Richards, R. J. (1987). *Darwin and the emergence of evolutionary theories of mind and behavior.* Chicago: University of Chicago Press.

Romanes, G. (1882). *Animal intelligence.* New York: Appleton.

Sherry, D. F. & D. L. Schacter (1987). The evolution of multiple memory systems. *Psychological Review, 94,* 439-454.

Staddon, J. E. R. (1987). Science and pseudoscience. *Interdisciplinary Science Reviews, 12,* 114-116.

Tulving, E. (1985). How many memory systems are there? *American Psychologist, 40,* 385-398.

Washburn, M. F. (1908). *The animal mind: A text-book of comparative psychology.* New York: Macmillan.