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Reciprocal Heuristics: A Discussion of the Relationship of the Study of Learned Behavior in Laboratory and Field

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At the turn of the century, the initiators of laboratory study of animal learning advocated two very different approaches to the subject matter. Willard Small favored the investigation of learning in ecological settings appropriate to individual species. E. L. Thorndike treated the process of association formation in animals as a general one, best studied in situations distant from those to which subject species were adapted. The latter view dominated laboratory study of animal learning for 80 years. The consequent absence of ecological content from laboratory investigations of animal learning, together with recent expansion in knowledge of the behavior of free-living animals, has created opportunities for ecologically sound investigations of animal learning of the type first advocated by Small. Studies of taste-aversion learning, although introducing evolutionary issues into the study of animal learning, do not exemplify such an approach. Integration of field and laboratory studies of behavioral plasticity in animals requires a change in the methods used to select phenomena for analysis. Such integration does not often lead to identification of the behavioral processes underlying the development of particular behaviors observed in nature. Rather, its results are an increase in the variety of learning processes investigated in laboratory settings and enhanced understanding of the behavioral capacities of subject species.

This paper is concerned with relationships, past and present, between laboratory and field studies of learning in animals. Discussion is presented in three parts: In the first, I describe two contradictory approaches to the laboratory study of animal learning advocated by its earliest students and the subsequent development of a tradition of investigation of animal learning without reference to ecological concerns. In the second, I discuss

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current opportunities for the study of animal learning provided by recent developments in behavioral ecology and field ethology. In the final section, research on social learning in animals is used to illustrate some difficulties which may be encountered both in extrapolating laboratory findings to field situations and in using laboratory research to analyze the processes underlying behavioral plasticity of animals in uncontrolled environments.

It is assumed throughout the present paper that the capacity to alter behavior as the result of experience is part of the adaptive equipment of organisms. Thus, it is assumed that the learning capacities of animals result from and are maintained by selective pressures acting on individual species in their respective ecological situations. On such a view, understanding of behavioral plasticity requires observation of learning in environments in which it normally occurs. Further, understanding of the behavioral adaptation of organisms to their respective environments requires investigation of the role of learning in promoting survival and fertility. Such an approach to the study of animal learning suggests that integration of the fields of animal learning and animal behavior will prove useful to both disciplines. It is therefore assumed that some degree of integration of these two historically distinct areas of inquiry is a goal worthy of pursuit by the practitioners of each.

PART I: THE DISTANT PAST

Publication of experimental studies of animal learning was initiated in North America at the turn of the century by Edward Thorndike (1898), Willard Small (1900a, 1900b) and Linus Kline (1898). It is traditional in histories of the study of learning to differentiate Thorndike's approach from that of his contemporaries in terms of their respective conceptions of the elements entering into associations (see, for example, Bolles, 1975; Jenkins, 1979). I would like, however, to call attention to other significant differences in the approach to the study of learning phenomena advocated by Thorndike and by Small and Kline (see also Timberlake, 1983).

Small's (1900a, p. 133) stated goal was "the careful description of the psychic properties of special animal forms," while Thorndike's purpose was to explore "the nature of the process of association in the animal mind" (Thorndike, 1911, p. 20). Thus, Small wished to begin with analysis of learning in individual animal species, predicting that "generalizations will come in due time" (1900a, p. 133). Thorndike, to the contrary, undertook the study of the general nature of association learning in animals, hoping to trace the origins of human intelligence by understanding development of mental life "down through the phylum" (1911, p. 22). His approach reflected a view of phylogeny, popular early in the present century (Romanes, 1884), that was subsequently discredited (Hodos & Campbell, 1969). In this view phylogeny consisted of an ordered hierarchy of living things and a progressive elaboration of intelligence as one ascended that hierarchy.

This fundamental difference in orientation was reflected in both the titles of the first experimental papers published by Small ("An experimental study of the mental processes of the rat") and by Thorndike ("Animal intelligence: An experimental study of associative processes in animals") and in their choices of experimental apparatus and procedures. Both Small (1900a, 1900b) and Kline (1898) explored the acquisition of habits that seemed important in their subjects' adaptation to natural conditions. Kline had studied hungry rats, employing what he thought might be their "dominant methods of food getting" (Kline, 1898, p. 277), gnawing or digging to acquire sequestered food. He argued that "a careful study of the instincts, dominant traits, and natural habits of an animal as expressed in its free life . . . should precede as far as possible any experimental study. Procedure in the latter case . . . must of necessity be largely controlled by knowledge gained through the former" (Kline, 1899, p. 399). For similar reasons, Small (1900a, p. 208) studied the learning of paths through complex mazes by wild and domesticated rats. He justified his choice of apparatus by reference to "the rat's propensity for winding passages" and a maze-like kangaroo rat burrow that he had seen illustrated in a popular magazine. Small argued explicitly that his apparatus allowed his subjects to exploit both their instinctive tendencies and previous sensorimotor experience in solving the problems he set for them. Thus, in the experimental work of both Kline and Small one sees a sincere, if unsophisticated, interest in studying animal learning within an ecologically appropriate context.

In contrast, Thorndike's selection of environments in which to study animal learning was determined by theoretical rather than ecological concerns. In accord with his interest in general processes of learning, Thorndike observed his subjects in puzzle boxes designed to study the formation of associations "free from the helping hand of instinct" (1911, p. 30). His approach was intentionally divorced from ecology; in Thorndike's view, association learning in pure form could be studied only in environments designed to reduce the role played by an animal's behavioral proclivities.

Small and Kline understood fully the implications of differences between their experimental procedures and those of Thorndike. Small's assertion, "Experiments must conform to the psychobiological character of an animal, if sane results are to be obtained" (Small, 1900b, p. 206), expressed an explicit rejection of Thorndike's approach to the study of association learning and its lack of reference to the natural circumstances of a subject species. Similarly, Thorndike's insistence on studying the behavior of animals in situations reducing the importance of the exercise of their behavioral predispositions led Kline to conclude that Thorndike's classic 1898 monograph cast light only on "animal psychosis" (Kline, 1898, p. 150). Questioning the relevance of results of studies of animals in environments failing to reflect ecological realities is not a modern development.

Influence of the Small–Kline ecological orientation toward the study of learning in animals is still evident in the early writings of Watson, "the laws of behavior in amoeba . . . must be determined and evaluated in and for themselves, regardless of their bearing upon such laws in other forms" (Watson, 1914, p. 27). In 1914, Watson was emphasizing the importance of the study of individual species, the need to use field studies to assess the adequacy of laboratory results to explain the behavior of subject species, and the importance of treating learning as an adaptive faculty.

Similarly, Clark Hull (1929) in an early paper on animal learning, questioned and discussed the adequacy of principles of acquisition and extinction uncovered in the laboratory to explain learned behaviors, such as predator avoidance, observed in nature (an issue later addressed by Bolles, 1970). Thereafter, Hull paid only lip service to ecological concerns in developing his model of association learning (Hull, 1937; 1943). Watson, in his influential later work, also abandoned his early position. "There is no such thing as an inheritance of capacity, talent, temperament, mental constitution or characteristics (Watson, 1924, p. 74)." Consideration of genetics, evolution, and ecology became largely irrelevant in the study of learning. Connections between the study of animal learning and many of the life sciences, fundamental to the ecological approach of Small and Kline, were almost entirely severed.

As Seligman stated many years later (1970, p. 406), "What captured the interest of the psychological world was the possibility that laws of behavior deduced from the study of animals in arbitrary situations might describe the general characteristics of behavior acquired as the result of pairing one event with another." Or, as Tolman asserted even more broadly in 1938 (p. 34), "Everything important in psychology . . . (save such matters as involve society and words) can be investigated in essence through the continued experimental and theoretical analysis of the determiners of rat behavior at a choice point in a maze" (Tolman, 1938, p. 34). The behavior of rats in T-mazes or pigeons in operant conditioning chambers was to serve the student of learning, as the inheritance of traits in drosophila served the geneticist or the functioning of the giant axon of the squid the neurophysiologist, as a convenient model preparation. So long as there was reason to believe, as Thorndike did, that similar processes underlay learning wherever it occurred in nature, the approach remained a reasonable one, consistent with basic methodology in the biological sciences.

For decades, study of learning processes as abstract entities both promised and produced broad empirical generalizations. This success contrasted sharply with the anticipated "botanizing" of learning phenomena which seemed an inevitable consequence of focusing, as Small and Kline had proposed, on specialized learning in individual species. Such generality was, however, achieved at a price. The untested assumption that the model systems selected for detailed analysis in the laboratory adequately reflected the learning capacities of animals artificially restricted the range of phenomena considered. Generality was achieved only by severely restricting the domain of discourse.

From 1920 to the present, the study of association learning within the general process view dominated the study of the behavior of animals by learning theorists. Study of the "psychic life of special animal forms" (Small, 1900a, p. 133) within ecologically relevant contexts was largely abandoned to ethologists and other biologically trained investigators. They undertook the study of learning as it occurs in nature with considerable energy and success. Perhaps most important, such studies of learning were, until very recently, carried out without reference to or influence upon experiments on associative processes undertaken in psychological laboratories (see, for example, Tinbergen, 1932).

The point of the preceding brief history is that at the inception of the study of animal learning two very different approaches to the subject matter were advocated: one treating the capacity to learn as but one element in the adaptive behavioral repertoire of individual species, the other focusing on learning as an abstraction to be studied by manipulation of signals, responses, and reinforcers selected without reference to the ecology of subject species. As any number of reviews have made clear, the latter approach carried the day.

It is only during the past decade, as possible inadequacies in the general process approach have become salient, that attention has again begun to focus on a more ecological approach to the study of learning phenomena. For example, Johnston's (1981) recent advocacy of task descriptions as a necessary antecedent to studies of animal learning, as well as his prediction that analyses of learning in natural habitats will lead to the discovery of local rather than global learning principles, represent both a return to the position of Kline and Small outlined above and a rejection of the general process view advocated by Thorndike.

PART II: THE RECENT PAST

Recognition by laboratory investigators of animal learning that study of plasticity in arbitrary situations might not lead to complete understanding of processes underlying behavior acquisition in natural circumstances is relatively recent. Though it need not have done so, such recognition attended the demonstration by Garcia and his co-workers of special features in the learning of taste–toxicosis associations by rats (Garcia, Ervin, & Koelling, 1966; Garcia & Koelling, 1966).

For some years prior to Garcia's discovery, there were available in the literature examples of animal learning which both defied interpretation in terms of the empirical generalizations resulting from decades of laboratory study of rats and pigeons and suggested the existence of specialized learning processes. To mention but a few of the better known examples: wasps learn the arrangement of landmarks surrounding their nest site during a single brief orientation flight (Tinbergen, 1932). Gobiid fishes learn the spatial relationships between the depressions and elevated ridges of their home territories by swimming over them at high tide and use the information thus obtained to leap from one tidal-pool to another if disturbed at low tide (Aronson, 1951, 1971). Bees acquire the capacity to compensate for the sun's movement in their navigation from hive to food source as a result of exposure to the sun's perceived movement (Lindauer, 1961). White-crowned sparrows acquire their species-typical songs and indigo buntings their migratory orientation as the result of exposure to specific sensory stimuli early in life (Emlen, 1970; Marler & Tamura, 1964).

The Garcia demonstrations of cue-to-consequence specificity (Garcia & Koelling, 1966) and tolerance of long CS–US delays in toxicosis conditioning (Garcia *et al.*, 1966) posed a particularly acute challenge to the prevailing general process view. Learning of taste–toxicosis associations could be discussed easily as an instance of Pavlovian conditioning, yet appeared to violate empirical generalizations derived from the study of logically identical instances of association formation. The anomalous learning was exhibited by laboratory rats rather than members of some unfamiliar species. Further, Garcia was a psychologist, publishing in psychological journals, and posing questions within established psychological frameworks. Thus his findings were harder to ignore and posed a more immediate challenge than the work of biologists, often studying unfamiliar species in unfamiliar paradigms, and publishing in journals and languages often unfamiliar to psychologists.

Interpretation of taste-aversion learning by rats as a specialized learning mechanism, reflecting the action of ecological demands (e.g., Rozin & Kalat, 1971), has served during the past decade as a bridge between those studying behavioral plasticity in laboratory and field. The taste-aversion learning preparation both brought to the fore the possibility that animals might exhibit learning processes shaped to meet environmental demands and introduced evolutionary issues into discussions of learning processes.

There is, however, a sense in which focus on taste-aversion learning has interfered with integration of laboratory and field studies of behavioral plasticity. Following Rozin and Kalat's (1971) forceful presentation of taste-aversion learning as a central component in the ability of rats to select nutrients, it became easy to forget that rats' facility in learning taste–toxicosis associations provides solutions for a problem that there is little evidence rats actually face in habitat undisturbed by man.

Garcia did not come to the study of taste-aversion learning as the result of field observations indicating that rats learn to avoid ingesting naturally occurring palatable-but-toxic foods that produce illness many hours after ingestion. Rather the capacity for taste-aversion learning over long delays was a serendipitous discovery in the course of explorations of the unconditioned effects of X irradiation. There is, unfortunately, little evidence either that rats encounter palatable-but-toxic foods in their natural habitat or that such toxins have effects delayed by many hours (Domjan & Galef, 1983). To the contrary, there are reasons to believe that the evolution of palatable toxins with delayed effects is less likely than that of vile-tasting, fast-acting poisons. Prey species which evolve means for manufacturing or sequestering toxins do so, at least in part, to deter potential predators. Immediately perceived unpalatability and rapid induction of illness or pain are more reliable deterrents to ingestion than palatability coupled with long-delayed negative aftereffects. The burden of proof of the existence of cryptic toxins that rats have had to learn to avoid for millenia in natural ecosystems rests on those who hypothesize their existence. Surely human progress in rodent control would benefit immensely from the discovery and use of concentrated cryptic toxins in poison baits. It is also somewhat disconcerting to find in the literature evidence that palatable, novel, toxic baits simply introduced into free-living populations of wild rats typically exterminate more than 75% of the target population (Chitty, 1954, Table 5, median result of poisoning 37 colonies).

The point of the preceding argument is *not* that in the field rats fail to learn to avoid both natural foods containing cryptic toxins and introduced poison baits. Perhaps they do. Rather, the point to be made is that in the absence of information as to the problems posed by environments with which rats have evolved to interact, explanations of behaviors in terms of their adaptive functions are working hypotheses and not explanations.

Further, there is no compelling a priori reason to believe that rats should have evolved to preferentially associate tastes, rather than other features of food objects, with toxicosis (Galef & Osborne, 1978). If, as has been argued, it is adaptive for chickens to be able to learn to avoid toxic foods on the basis of their appearance, it is hard to understand why it would be disadvantageous for rats to do so. The assertion that organisms most readily learn aversions to foods using those sensory modalities which are primary in selection of ingesta (Rozin & Kalat, 1971) does not, even on the basis of the restricted range of species examined, seem a sound empiric:ralization. *Buteo* hawks, surely at least as visually guided in the selection as chickens or quail, develop stronger aversions to thethan to the visual properties of prey (Brett, Hankins, & Garcia, 1he cavy, like the rat, crepuscular in its daily activity rhythm, formsons to both the taste and visual properties of foods (Braveman, 1Chickens exhibit strong aversion learning to the taste of fluids, but nos (Gillette, Martin, & Bellingham, 1980). It is difficult to argue that specializations could have been predicted from what is known of isory systems employed in food selection by members of various s.

The laboratory study of animal ig does not become ecologically sound as the result of ad hoc funcexplanation. *Just So Stories* are as questionable when generated inise to laboratory as to field data. Meaningful integration of laboratofield studies of behavior requires a reorientation in the developmenestions rather than a paragraph or two of untested (and frequentestable) speculation as to the adaptive significance of behavioracities of organisms observed in experimental situations.

Those of us currently engaged study of acquisition processes in animals in laboratory settings :erested in a more ecologically sound approach are fortunate in twrds. First, both the breadth and depth of the ecological literature hoanded manyfold since the days of Small. There are now described iterature any number of instances of apparent behavioral plasticity iliving animals amenable to investigation in laboratory settings. Sove already attracted considerable attention by laboratory workers (e.gecognition (Holmes & Sherman, 1982; Kareem & Barnard, 1982; Pcepper, & White, 1981), search–image formation (Pietrewicz & Kam), scatter–hoard location learning (Shettleworth, 1983)). Many othe., mimicry, homing, predator avoidance, or individual recognitive yet to be brought into the psychological laboratory.

Second, field workers have bere concerned to elucidate the adaptive function of the behaviorsobserve than to investigate the behavioral processes responsible 1development or acquisition of those behaviors. In those cases whrning is invoked in explanation of the development of some behattle attempt has been made to distinguish the effects of simple expclassical or operant conditioning, habituation, latent learning, incidenting, imprinting-like phenomena, etc. Clearly, those interested in anaf proximal processes underlying behavior acquisition have the oppo to make a contribution to the understanding of the developmentaptive behaviors exhibited by animals in nature. However, a coible rethinking by investigators of learning in the laboratory of thea used in selecting phenomena for analysis is required if this oppy is to be grasped.

Extension of the study of animal learning to investigation of phenomena observed in natural settings provides opportunities beyond simply filling a "niche" left temporarily vacant by field investigators. Laboratory study of animal learning has been motivated throughout its history by the conviction that certain pervasive phenomena of learning are captured in classical and operant conditioning paradigms (Jenkins, in press). Such laboratory studies have been sustained by the expectation that rules or laws of learning discovered in explorations of abstractly conceived laboratory preparations would be sufficient to explain much of the behavior of organisms outside the laboratory. Unless one believes that the study of learning in the laboratory is a worthwhile end in itself, it is necessary to explore the adequacy of principles of learning deduced from laboratory studies to explain instances of behavior acquisition in extralaboratory environments.

Recent developments in the study of human cognitive processes suggest that the utility of laboratory studies of animal learning for the understanding of human behavior may be restricted. Much of human behavior reflects linquistic and cognitive capacities that may not be adequately reflected in either classical or operant conditioning paradigms (see, for example, Brewer, 1974). There are reasons to hope that principles derived from laboratory studies of conditioning in animals will prove useful in explicating acquisition processes exhibited by animals in nature. However, agnosticism is the appropriate stance until the utility of laboratory principles in interpreting acquisition processes exhibited by animals in native environments has been demonstrated. Classical and operant conditioning must occur outside as well as inside the laboratory (Croze, 1970; Hollis, 1982). There is, however, some question as to how much of the behavioral plasticity of animals responding to the challenges posed by the environments in which they evolved reflects these processes.

It has become evident in recent years that study of animals in standard laboratory paradigms leads to systematic underestimation of the richness and subtlety of their capacities to learn about their environments. Models of animal learning will have to be developed that encompass this richness and offer some insight into underlying mechanisms, or the usefulness of the laboratory approach will be rapidly undermined. Such phenomena as the apparent ability of Clark's nutcracker to remember the locations of hundreds of food caches (Balda, 1980) or of tits and chickadees to remember the location of tens of cached seeds (Sherry, Krebs, & Cowrie, 1981) should lie within the purview of learning theory. Similarly, the behavioral mechanisms responsible for the efficiency of a variety of predators in selecting foraging sites and prey of different sizes suggests learning capacities that would be unexpected given traditional models of animal learning (Kamil & Sargent, 1981). Such phenomena both pose a challenge and provide an opportunity. The challenge is to the adequacy the result of perceptual learning (Sluckin, 1964) or simple exposure effects (Hill, 1978) that have not been explored in any detail by students of animal learning. Although such phenomena can sometimes be discussed as instances of classical conditioning (Hoffman, 1978), it seems more likely that they represent instances of a third type of learning which has failed to capture the attention of the psychological community.

I take two general messages from the above. First, that although field observations can point to instances in which learning occurs, they may provide little information on how that learning proceeds in complex environments. Second, although laboratory experiments may demonstrate behavioral capacities of an organism, they do not provide unequivocal evidence that those capacities are used by free-living organisms to solve a particular problem.

In sum, field observation can provide evidence that members of a species learn to solve some problem; laboratory studies can demonstrate behavioral capacities of the target organism allowing for solution. However, it may be very difficult to determine if or when a given capacity is actually used in nature to solve a particular problem. One might, for example, observe a group of young rats eating the same diet that their mother had been eating and know that the young could be influenced in their diet choice in all the ways mentioned above. Yet how would one know in any particular case which of several potential mechanisms were influencing the young rats' diet selection? Perhaps even more disconcerting, if the laboratory study of the behavioral processes responsible for social influence on diet selection had proceeded to the point where only a single process for social influence were known, the observed behavior would be attributed to that process both with confidence and without justification.

Evidence of multiple behavioral processes with a final common outcome is unlikely to be limited to social learning phenomena. Studies of behavioral processes underlying, for example, homing in pigeons (Schmidt-Koenig & Keeton, 1978) or kin recognition in Belding's ground squirrels (Holmes & Sherman, 1982) similarly reveal multiple processes capable of supporting development of the same observed behavior. Further, it is unlikely that the boundary conditions within which various processes operate will prove to be nonoverlapping. In consequence, the most obvious potential contribution of laboratory research to the understanding of behavioral phenomena observed in the field, determination of the behavioral processes responsible for the development of particular behaviors observed in free-living animals, may in general be difficult to accomplish. This is no cause for despair. Living systems are complex and redundancy in the mechanisms underlying the development and expression of behavior is one facet of that complexity. The resultant ambiguity in the applicability of laboratory findings to field observations can be reduced only by increasing both the ecological relevance of laboratory paradigms and the precision of field observations. Continued and expanded interchange between laboratory and field workers is the catalyst for potential progress.

Field observations can point to areas in which organisms express special competences, suggesting the existence either of refinements of known learning processes or previously unsuspected learning mechanisms. Laboratory investigations of plasticity can expand (or limit) the range of acceptable proximal explanations of changes in behavior observed in the field. Field studies can thus direct laboratory research on animal learning toward potentially fruitful areas of investigation, while laboratory research can provide assistance to field workers in understanding the behavioral mechanisms that might be responsible for the acquisition or development of adaptive responses. Although the use of laboratory investigation for the reductionist analysis of field phenomena is not likely to result in logically compelling outcomes, each of the two approaches to the study of behavior can serve as a useful source of working hypotheses to the other.

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