

# COMPARATIVE COGNITION & BEHAVIOR REVIEWS

## Learning Theory for Comparative Psychologists

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This article offers a brief and simplified guide to the basics of learning theory. Certain central topics are described: classical conditioning, instrumental (operant) conditioning, extinction and inhibition, discrimination, and biological constraints on learning. A proper how-to guide would spell out how the findings and theories described under these headings can be applied to the explanation of phenomena in animal cognition, but that is an ambition rather than an achievement to be described (and the work is perhaps best left to others engaged directly in the study of animal cognition). Nonetheless, this article expresses the hope that learning theory will not be seen as an alternative to cognitive processing but rather will form part of a full account of the mechanisms involved in such processing.

*Keywords: learning theory, conditioning, extinction, discrimination, biological constraints*

It will be well to define our terms. *Learning theory* is perhaps straightforward, at least if we are content with a definition derived from pointing to examples. This approach dominated psychology in the United States throughout much of the 20th century and is exemplified by the work of Hull, to whose name it is customary to add Guthrie, Tolman, Spence, and perhaps a few others (see Bouton & Boakes, 2019). Learning theory is characterized by the intensive study of the behavior of a laboratory animal, usually a rat or pigeon, under conditions in which environmental factors can be fully controlled by the experimenter. The aim is to determine psychological principles of general relevance. A parallel can be drawn with a biologist who chooses a model system (such as the fruit fly *Drosophila*), carries out experimental procedures (in this case, controlled mating) under controlled conditions, and aims to find laws (in this case, of genetics) of general applicability.

After much debate in the first half of the 20th century, learning theorists settled on a fairly widely agreed set of findings and theoretical principles (well summarized by Mackintosh, 1974) that drew not only on the work of

U.S. behaviorists but also, importantly, on that of Pavlov and Konorski. This consensus position is often referred to as associative learning theory, given that the postulation of connections among entities representing stimuli and responses plays a central role (although it is notable that its account of the role of motivational factors is of equal importance). There is no need to say more at this stage, given that the rest of this article presents this form of learning theory in greater detail. It is necessary, however, to add the name of Skinner, whose version of “learning theory” (starting with Skinner, 1938) would deny the usefulness not only of the concept of learning but also of the notion of “theory” itself. But like the other learning theorists just mentioned, Skinner’s practice was to study the behavior of a model system under controlled conditions—typically a rat or a pigeon in the “Skinner” box—to established generally applicable principles of behavior.

*Comparative psychology* is an altogether more slippery notion. From its very origins (ever since Romanes persuaded his sister to look after a young monkey so that he could chart its mental development; see Boakes, 1984)

empirical, scientific psychology has concerned itself with the behavioral or mental functioning of nonhuman animals. J. B. Watson himself, who might be regarded as the grandfather of learning theory, cut his scientific teeth by studying the behavior of terns in their natural habitat (the Dry Tortugas of the Caribbean, between Florida and Cuba). Work of this sort was referred to as comparative psychology. There was no suggestion that this necessarily involved the explicit comparison of different nonhuman species (the sort of research program pursued in the mid-20th century by M. E. Bitterman (e.g., Bitterman, 1965). Rather, the comparison was implicitly made with the behavior or mental functioning of humans; by this token, any study with a nonhuman animal counted as “comparative.” Given that, as the 20th century progressed, much of the work with nonhuman animals was conducted in the conditioning laboratory, it is no surprise that the term *comparative psychology* became almost synonymous with *learning theory*. Thus, until it ceased publication (in 1974), the primary journal for the publication of work in learning theory was the *Journal of Comparative and Physiological Psychology*. Again, when in 1966 zoologist R. A. Hinde published his influential book *Animal Behaviour*, his subtitle—“A Synthesis of Ethology and Comparative Psychology”—conveyed a wish to bring together the work of ethologists with that of learning theorists.

Things began change in the 1970s. When Wasserman (1981) entitled a book review “Comparative Psychology Returns,” he wanted to announce what he referred to as a “veritable renaissance” of comparative psychology (p. 243). The essence of this was the view that “in order to advance our understanding of behavior, it is useful to consider processes and activities, generally called cognitive, that may intervene between changes in the environment and changes in overt behavior” (p. 243). The book in question was that entitled *Cognitive Processes in Animal Behavior*, edited by Hulse, Fowler, and Honig (1978). And according to Wasserman and Zentall (2006), who edited a similar volume some years later, this book led to the creation of a new field of research—comparative cognition—which entails the rigorous scientific study of animal intelligence (including perception, spatial learning, memory, timing, categorization, concept formation, and rule learning). Slightly worrying, for the present purposes, is the fact that Wasserman and Zentall went on to say that this approach had the effect of “freeing interest in complex

behavior and learning from the grasp of the rigid theoretical structures of behaviorism that had prevailed during the previous four decades” (p. v). If these “rigid theoretical structures” are taken to be those of the learning theorist, then the student of comparative psychology (or cognition) has nothing to learn from learning theory apart from the best way of escaping from its “grasp.” But that is not a topic for debate at this stage. Rather, at this point we need a statement of the essential notions of learning theory so that each student of comparative cognition can decide for him- or herself whether these are useful in advancing their research programs.<sup>1</sup>

### *The Basics of Learning Theory*

The text that follows attempts to present, in just a few paragraphs on each topic, a summary of the current state of learning theory—its concepts and findings—along with a few references that will allow interested readers to follow up lines that might be relevant to their work in comparative cognition. Most of the work described comes from the study of a few laboratory species, making it pertinent to ask whether the findings will be fully relevant to the wider range of species often used in work in comparative cognition. It is some comfort, therefore, that the extensive survey provided by Macphail (1982) shows that the basic learning phenomena to be discussed here can be obtained in species from all major vertebrate groups.

I have not given a reference for each fact or notion that is presented. For a more extensive list of relevant references under each heading, the reader can turn to that produced by Bouton and Hall (2019) in their contribution on learning theory in the online series of Oxford Bibliographies. The topic headings used next are (more or less) those used by Bouton and Hall in that bibliography.

### *Classical Conditioning*

Most of the phenomena that intrigue us as psychologists studying the behavior of others (humans as well as other species) occur when the animal interacts with some aspect of its environment and is changed by the experience, so that it behaves differently, even when confronted with the same environmental conditions. With classical

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1. In fact, inspection of the content of the various chapters of Wasserman and Zentall (2006) is reassuring in this respect, as the majority of the contributions are well informed about learning theory and willing to make use of its methods and findings. The chapter by Hulse (2006) provides a thoughtful personal reflection on learning theory and the development of comparative cognition.

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conditioning, in which a light (say) evokes one response on first presentation (an orienting response) but a different response (salivation) if the presentation has been followed by food, Pavlov (e.g., 1927/1960) gave us a model system that demonstrates the phenomenon and allows experimental examination of the mechanisms involved.

*Varieties of conditioning and the form of the conditioned response.* Taking the defining feature of classical conditioning to be that one stimulus accompanies (usually precedes) the presentation of another allows for consideration of a wide range of procedures (and outcomes). Some are close to Pavlov's original, as when presenting a brief tone to a rabbit prior to a puff of air to its eye, the *unconditioned stimulus* (US) allows the tone to come to evoke the eyeblink response. In others, the form of the *conditioned response* is less predictable, as when a pigeon trained in the autoshaping procedure starts to "eat" the illuminated key that precedes food delivery. A rat given a brief electric shock to the feet will give a sudden jump, but if the shock has been preceded by another event such as the sounding of a tone, that *conditioned stimulus* (CS) will evoke the response of freezing. In flavor-aversion conditioning, the conditioned response is the absence of a behavior—the refusal to consume a foodstuff or a flavored drink that has previously been associated with a state of nausea. In some procedures, the conditioned response is found to be quite the opposite of that evoked by the US. A dramatic example is the opponent (or compensatory) response that can be evoked by cues associated with an injection of insulin; in this case, the conditioned response is an elevation of blood sugar level (i.e., the opposite of the effect produced by insulin itself). Phenomena of this sort have prompted the development of a "functional" approach to classical conditioning (see, e.g., Hollis, 1982, 1997) that emphasizes the adaptive biological significance of conditioning, with the conditioned response serving to help the animal cope better with an upcoming event.

Whatever the merits of the functional approach, it should be noted that not all conditioning arrangements generate an obvious conditioned response. In the phenomenon known as *sensory preconditioning*, it is possible to show that pairings of two stimuli, neither of which evokes any obvious response, can change their properties in a way best understood if we accept that the first becomes linked or associated with the second, making it able to activate some representation of the second. The notion of association has long played a role in the analysis of psychological functioning offered by (some) philosophers. Accepting this interpretation of classical conditioning allows the

view that the fact that, often, the procedure evokes an overt conditioned response is something of a convenient accident—convenient because it makes conditioning an ideal test bed for working out empirically, the "laws of association" that were only postulated by the philosophers.

*Factors affecting conditioning: Theories of association formation.* Although the specific training procedures may be very different, the same set of factors determine acquisition of the conditioned response in all. Unsurprisingly, acquisition depends critically on the number of pairings of the stimuli, their intensity and duration, and their temporal relation (for a review, see Hall, 1994). These dependencies can be readily accounted for by the proposal that pairing the stimuli allows a link to form between their central representations (sometimes referred to as "nodes"). The parameters that most effectively produce conditioning (in allowing the CS to acquire *associative strength*) are those that ensure appropriate activity in the two nodes at the same time. This simple principle of *contiguity* forms the basis of the account of association formation proposed by Wagner (1981) and to be described next. There are, of course, other interpretations of conditioning available, but this version deserves our special consideration as it possesses, in all major respects, those features that one comparative psychologist (Roitblat, 1987) has put forward as defining what he called "the standard associative model."

It is perhaps surprising that a theory of this sort can be developed to accommodate the fact that simple contiguity is not enough to ensure association formation. The classic demonstration is that provided by the phenomenon of *blocking*: the observation that acquisition to stimulus A will be blocked, will fail to occur, if it is presented in compound with another (B) that has already been trained and has acquired associative strength. Put informally, A will not acquire strength if the outcome of the trials is not surprising (being signaled by B); or, almost equivalently, a stimulus, like A, that supplies no new information will not be learned about. Wagner's theory readily accommodates this result by its assumption (justified on other grounds) that a node that has already been activated associatively (in this case, by way of stimulus B) cannot be activated in the normal way by the application of the stimulus to which it is normally sensitive. Stimulus A, therefore, will not be able to form an association with the node normally activated by the US. This is not to say that "US surprisingness" or "CS information value" play no role in conditioning; rather, it may be interpreted as providing a specification of the mechanisms that underlie these cognitive concepts.

More problematic for a theory of this sort are the many studies showing that conditioning is sensitive to the extent to which the stimuli are already familiar. Conditioning will be retarded both by prior exposure to the CS (known as the *latent inhibition* effect) and by prior exposure to the US (known, unimaginatively, as the US-preexposure effect). Attempts to explain these effects in terms of simple associations (usually between the context and the event presented in it) have proved unsatisfactory. Latent inhibition, in particular, seems to be best explained in terms of the suggestion that the “associability” of a stimulus—that is, its ability to govern attention, or at least that aspect of attention necessary for conditioning to occur—can be modified by experience.

The suggestion that the attention paid to a possible CS can be modified by experience has given rise to formal accounts of conditioning (beginning with Mackintosh, 1975; also Pearce & Hall, 1980) that are intended to deal not only with latent inhibition but also with conditioning generally (i.e., the processes of excitatory acquisition described earlier and, in the case of Pearce & Hall, the effects of inhibitory learning and extinction, to be discussed shortly).

It is worth noting that theories of this sort (see, e.g., George & Pearce, 2012; Hall & Rodriguez, 2010, 2019) have been developed to deal with the properties and function of “attention” more generally, making them theories concerned not simply with association formation but with the properties of a set of important cognitive processes, which go under the heading of “attention.” Perhaps this term is best seen as a label covering a range of mechanisms specified by the properties of parameters in the formal theories. Hall and Rodriguez (2010, 2019), for instance, distinguish the attentional process that determines how well an event is learned about, from the parameter that determines the vigor of the response the stimulus will elicit. Labelling their account as “attentional” is useful when it comes to communicating the general area of interest; the cash value of the attentional theory lies in its specification of the properties of the various parameters of the formal model.

The theories just described have been developed primarily on the basis of the investigation of simple associations involving just a pair of events (CS and US). It is important to note, then, that the “conceptual nervous system” implied by this analysis is not restricted to this simple structure. Rather, it is assumed that there will be whole range of nodes representing a myriad of stimuli with a complex network of links connecting them. And these links, it must be supposed, can do more than simply

excite activity in a node. For example, the phenomenon of *occasion setting*, to be discussed in the next section, can be explained if it is allowed that activation of a node might produce not an observable response but rather modulation of activity in the link connecting two other nodes. There may also be nodes (“hidden units”) that are connected only to other nodes (i.e., are not directly activated by stimuli and do not evoke an observable response) and that serve a purely computational function. This general scheme will be familiar to psychologists who have come to it not by way of the learning laboratory but from the perspective offered by artificial intelligence. The successes of “connectionism” demonstrates how complex cognitive phenomena can be derived from relatively simple mechanisms (if you have enough of them).

### *Instrumental (or Operant) Conditioning*

We turn now to learning procedures in which the animal’s behavior is instrumental in determining what happens. We owe the notion that such procedures would result in learning—that an animal’s behavior will be modified by its consequences—largely to the work of comparative psychologists. C. L. Morgan presented the principle in his book *An Introduction to Comparative Psychology*, first published in 1894. He drew on his experimental studies with chicks, but he is perhaps best known for his report of observations made of his pet fox terrier (Boakes, 1984). And the early studies of Thorndike, Morgan’s near contemporary, were genuinely comparative involving cats, domestic chicks, monkeys, and dogs. But his “law of effect” was found to apply to all of them. That is, for all, the likelihood of the occurrence of a particular item of behavior (still referred to as a response, in spite of the absence of a clear eliciting stimulus) will be determined by its consequences—by the *effect* it has. A rewarding outcome (e.g., food for a hungry animal, escape from confinement) will increase the likelihood of the response, will serve as a *reinforcer*. Some theorists have been concerned by the obvious circularity of defining a reinforcer as an event that reinforces. Others, notably Skinner, have put this on one side and got on with the job of analyzing in detail how behavior is determined by its effects. The results of his atheoretical program of research in what he termed the “experimental analysis of behavior” will contribute to the arsenal of techniques used in experimental studies by comparative psychologists. For theoretical notions that might be used in the explanation of behavior studied by comparative psychologists, it is necessary to turn again to an associative analysis.

*Associative accounts.* In instrumental conditioning, the animal does something (a response [R]) in a certain situation (in the presence of a stimulus or stimuli [S]), and the R produces an outcome (O) of some sort. (The rat presses the lever and receives a food pellet.) Early accounts focused on the possibility that S–R associations would form in these circumstances, but there is no reason to suppose that the other events are incapable of joining in. After all, an S–O association is just what we suppose is formed in classical conditioning, because we can treat the outcome as being effectively a US that follows the presentation of a set in environmental stimuli (the CS). And if the central representation that equates to the emission of some action (R) can become linked to a preceding S, why should it not also become linked to a stimulus (O) that follows it?

Early theorists (such as Thorndike) emphasized the role of the S–R link, an account that has the advantage of supplying a mechanistic account for the emission of the response. (The S is assumed to elicit it.) But in this account the effect of the O is simply to fix the S–R connection. It has no explanation, then, of the many studies (summarized by Dickinson, 1985, and by Colwill & Rescorla, 1986) showing that the O does more than support association formation but is itself is learned about. Specifically, when the positive value of a food used as O is reduced or reversed by a classical conditioning procedure, such as inducing a state of nausea after consumption of that food, the likelihood of performing the R is often found to go down. This would not happen if the behavior depended solely on an S–R connection—once this has been formed, the current value of the O would be irrelevant. The behavior appears to be *goal-directed*, depending on information about the relationship between R and O, rather than the *habit*, implied by the S–R account. Interestingly, this effect depends on the details of the schedule of reinforcement used in training and the duration of that training. Extended training with a simple schedule in which every response is reinforced can produce responding that is resistant to reinforcer devaluation (Adams & Dickinson, 1981). Under such circumstances, the importance of the R–O relationship is reduced and the behavior has transitioned from goal-directed action to a habit.

*Pavlovian–instrumental interaction.* We have already noted that classical (Pavlovian) conditioning will occur during instrumental training, as the contextual cues of the training situation will become associated with those stimuli that constitute the (R-produced) outcome. The role played by classically conditioned stimuli in instrumental

performance has been investigated by experiments in which classical conditioning is conducted separately, outside the instrumental training situation, and then the CS is presented in that situation. Some effects obtained with this procedure reflect the direct interaction of the instrumental response with the conditioned response evoked by the CS (if a rat freezes in response to a CS associated with shock, it will not be able to press a lever for food reward). But not all the observed effects can be explained in this way; rather, they reflect the ability of the CS to modulate the motivational state of the animal (see, e.g., Konorski, 1967). Thus, a CS that has signaled shock can enhance performance based on avoidance of shock but will inhibit the positive motivation that underlies responding for an appetitive outcome. And a CS that has signaled a positive outcome can enhance the vigor of instrumental responding supported by reward.

Such Pavlovian-instrumental transfer (PIT) can be quite general so that, for example, a CS associated with one positive outcome (say, one type of food) will enhance instrumental responding for another (a different food), presumably because both R–O associations are energized by the same appetitive motivational system. But there is also a specific aspect to PIT (see, e.g., Carboni et al., 2016) in which a CS associated with, for example, a given food type will selectively enhance the response producing that type rather than some other. Work on PIT has had substantial comparative importance, comparative in the old sense of having relevance to the behavior of our own species. Specifically, a parallel has been drawn between specific PIT and the effects of cues associated with alcohol or drugs of abuse in promoting the (instrumental) behavior that leads to a relapse in individuals seeking to abstain.

*Occasion setting.* Operant responding can come under the control of stimuli; if the response generates the food only when a light is on, the animal will come to respond only in the presence of the light. Having rejected the associative S–R analysis, Skinner opted for the description that in these circumstances the stimulus “set the occasion” for responding. In associative terms, this has been interpreted as meaning that the animal learns about the hierarchical relationship between the stimulus and the response-outcome association: [S – (R-O)]. Here the S represents an occasion setter, a stimulus that is not directly associated with the other events but that activated or facilitates the associative link between them. This extension of associative theory has greatly expanded its explanatory power (see Schmajuk & Holland, 1998).

Although the term *occasion setting* was introduced in the context of operant conditioning, there is no reason to think that the proposed mechanism will be confined to this training procedure. In classical conditioning, the effectiveness of a CS–US association has been demonstrated to depend on the properties acquired by another cue that was present when the original CS–US pairings were given (Holland, 1992); and again the most widely accepted explanation is that the added cue works to enable the ability of the CS to activate directly the US representation. Such higher-level control of the working of associations may be the rule, rather than the exception, even when there is no training with a specific cue as the occasion setter. Many of the effects produced by conditioning procedures prove to be context dependent; that is, they transfer only poorly when a test is given in a different place. The disruption produced by the novelty of a new context is sometimes to blame, but some cases such failure of transfer has been found to depend on the conditional control exerted by contextual cues—or more accurately, on the lack of such control when the context has been changed (Hall & Mondragon, 1998).

A full account of the range of complex associative structures that can be established, once the role of occasion setting is taken into account, is presented in Hall (2002). This deals not only with instrumental conditioning but also with conditional cue effects in classical conditioning.

### ***Extinction and Inhibition***

The extinction procedure involves omitting the US in classical conditioning or omitting the outcome in instrumental conditioning. In both cases the response established by reinforced training declines in strength or frequency. It is tempting to think that in extinction the changes acquired during acquisition are simply erased, but there is plenty of evidence that this is not so—that the original learning is preserved but that its ability to influence behavior is suppressed by some new learning.

The phenomenon of *spontaneous recovery* neatly shows that extinction does not erase the previous leaning. The term refers to the fact that an item of behavior that has declined after undergoing extinction will return, even if not with full vigor, if an interval is left between the extinction procedure and the retest. The effect is explained in terms of an inhibitory learning process engaged by the omission of the expected outcome or US. For classical conditioning, it has been suggested that the CS acquires the ability to *inhibit* activation in of the representation of the US, perhaps, by way of the formation of a new association with some representation of the omission of the US (Konorski, 1967).

The excitatory association acquired initially remains (more or less) intact during the extinction procedure but is suppressed by the inhibitory process, becoming evident again when the (presumably evanescent) inhibitory process dissipates with time, or with the change of context that is a consequence of the passage of time. Further evidence comes from the demonstration that the effect of the extinction procedure has been found to be dependent on the specific physical context in which it occurs, probably because the context comes to act as an occasion setter controlling the effectiveness of the inhibitory learning. With a change of context (i.e., giving a test in a different place), behavior that has apparently been lost as a consequence of extinction, will reappear (see Bouton, 2017).

It is possible to conduct the extinction procedure with an event that has not had prior training. This is a contorted (but possibly illuminating) way of saying that it is possible to present an initially novel stimulus repeatedly without it being followed by any other event. The result is that such a stimulus is retarded in further learning, as when, for instance, it is trained as a CS in classical conditioning. This phenomenon has been called latent *inhibition*, although as we have already seen, an alternative interpretation—that the effect depends on a reduction in the ability of the stimulus to command attention—has been more popular. It is widely accepted, however, that “true” inhibition can be generated if the novel stimulus (call it N) is presented in compound with a CS that has previously undergone excitatory conditioning (call it A). After this treatment, stimulus N is found to be retarded in acquiring excitatory strength when subsequently used as a CS in excitatory conditioning; and will be able to suppress the ability of a separately trained CS to evoke its CR. This is the outcome predicted by associative theories that give a central role to the notion of “prediction error.” In the phase of compound training, A predicts a US that fails to occur. Acquisition of inhibition by both N and A will reduce this prediction, adjusting the animals’ expectations to match the prevailing conditions. The effect on stimulus A will be just to offset the excitatory power previously acquired, leaving A neutral. But for stimulus N, which comes to this procedure with no initial excitatory strength, the result will be a stimulus that has net inhibitory properties (see, e.g., Rescorla, 2006)—a signal that no US will occur.

### ***Discrimination***

*Generalization and discrimination.* A pigeon trained by operant techniques to peck at a light of a given color will show a reduced rate of response when the wavelength is changed, as there is an orderly decline as the wavelength

moves away from the initial value. That is, training with one color will *generalize*, to some extent, to another. The fact the responding to the test stimulus is reduced shows that the animal can *discriminate* that stimulus from the one with which it was trained. It is important to note that, as with any null result, the failure to find an effect does not prove its nonexistence. Pigeons trained in the presence of a given tone will show perfect generalization to tones of a different frequency, but we would be wrong to conclude that they cannot discriminate tonal frequency. If the birds are trained with food available only when the tone is on and not when the tone is absent, then a subsequent test with different frequencies will reveal sloping gradients of generalization. One interpretation of this finding is that this training procedure reduces the likelihood that contextual cues will gain control over behavior—simply being in the context is no longer a good predictor of reinforcement—and that this allows better learning about the auditory cue that occurs in that context.

*Discrimination learning.* The procedure in which one stimulus is associated with reinforcement and another (the absence of the tone in the case just described) is associated with a different outcome (usually, as in this case, with the absence of reinforcement) is known as *discrimination training*. Analysis of the processes responsible for discrimination learning is of special relevance to our present concerns, in that, almost a century ago, it provided a battleground for a contest between rival accounts that differed in their willingness to use cognitive concepts in their explanation of the phenomena. Krechevsky (1932) published a paper on the behavior of rats trained on a simultaneous discrimination—that is, given a choice between the two stimuli. The publication was titled “‘Hypotheses’ in Rats.” The somewhat defensive or apologetic scare quotes does not really detract from his conclusion that in learning such a discrimination the rat tries out a set of possible solutions and that “the learning process . . . consists of a series of integrated purposive behavior patterns” (p. 532). The response to this account offered by Spence (1936) was hugely influential. Spence demonstrated how the patterns of behavior regarded by Krechevsky as instances of hypothesis testing could be explained in terms of the acquisition or loss of associative strength by the various stimuli faced by the rat learning a simultaneous discrimination. Whether his account should be considered an alternative to the cognitive account or a specification of the mechanisms underlying cognitive processes is a matter for debate.<sup>2</sup>

*Attention.* In spite of its successes, there is no doubt that an associative analysis (of the sort offered by Spence, 1936) is incomplete as an account of discrimination learning. Spence had been anxious to exclude any notion of attention from his account of discrimination learning; in his day, the notion of attention was often taken to imply some (unexplained, and possibly inexplicable) force that selected some events for special treatment. But it is clear that one event (say, a loud tone) will be more salient than another (a soft tone) and thus be more likely to command the processing required for it to function in learning (say, as a CS). And it does not require an appeal to unexplained forces to postulate that certain training procedures might change the effective salience of a stimulus (i.e., the ability of the stimulus to command attention). The effect can be demonstrated by studies of the transfer of training, using a procedure pioneered by Lawrence (1949) to demonstrate what he referred to as the “acquired distinctiveness of cues”. Lawrence showed that discrimination training with one set of cues could enhance performance when the subjects were required to learn a quite different task involving the same cues. More recent demonstrations of the same basic phenomenon have been provided by Le Pelley and McLaren (2003) using human subjects, and by George and Pearce (1999) using pigeons, who showed that positive transfer could occur to new stimuli, provided these differed along the same dimension as those used in original training.

In spite of these interesting effects, it might still be argued that Spence was wise to be wary of the notion of “attention” in the context of learning theory. The results just discussed can be taken as showing that the power of a stimulus to attract attention can be enhanced when it is reliably associated with a reinforcer. But there are also well-documented effects from studies of simple classical conditioning (see Pearce & Hall, 1992) to show that some aspect of attention will decline under these circumstances but will be maintained when the consequences of the stimulus are uncertain. This result serves to confirm what was said previously with respect to classical conditioning—that “attention” is fine as a chapter heading, but formal theorizing requires a more complex account. More generally, the implication is that the cognitive concepts that are

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2. Something similar appears to have occurred more recently in the case of spatial learning, where accounts in terms of complex cognitive processes have been challenged by attempts to explain the phenomena by way of the standard mechanisms employed by learning theorists (see Mackintosh, 2002).

satisfactory for the informal analysis required in everyday life may prove inappropriate, even misleading, when we come to a formal analysis based on the experimental study of animal behavior.

### ***Biological Constraints on Learning***

This section has an odd phrase as its heading (What aspects of an animal's behavior are not constrained by its biology?), but the term became popular after work in the 1960s demonstrated that some combinations of CS and US, and of response and outcome, were learned about readily, and others rather poorly. The classic instance concerned aversive conditioning in rats; the finding was that rats were very ready to associate sickness with a taste and a footshock with an auditory cue, but that the other combinations (noise–sickness, taste–shock) were difficult to establish. The rapidity of taste-aversion learning fits with the biological needs of the rat; a nocturnal omnivorous animal needs to be able to identify foods that might be poisonous, and evolution appears to have done what is needed. The notion that (at least some forms of) learning might be “prepared” by the evolutionary history of the species (or genus, or family, or order), and might follow unique rules, constitutes an obvious challenge to those seeking principles of cognition applicable across a range of species. From their different perspectives, this could be a matter of concern for both the learning theorist and the comparative psychologist.

The initial response to effects of this sort (see, e.g., Rozin & Kalat, 1971) was that instances of learning studied in the laboratory were likely to reflect specific adaptations to specific problems—that the “laws of learning” were no such thing, quite lacking in generality. Fortunately, at least from the perspective of those seeking general laws, this extreme view has not stood the test of time. Further research has substantially confirmed the view that taste aversion learning (and other apparently specialized forms of learning) follow the known “laws” derived from the study of other learning procedures (Domjan, 1983). In this context it is pertinent to note that studies of learning in honey bees (e.g., Bitterman, 1996) have shown that they can learn about the relation between olfactory and visual cues and sucrose reinforcement in ways that closely match the effects found in vertebrates. The implication is that the constraints imposed on an animal in having to adapt to its environment are sufficient to establish the same basic mechanisms in a range of species even though the “hardware” (the brain of the bee evolved independently of the vertebrate brain) may differ substantially.

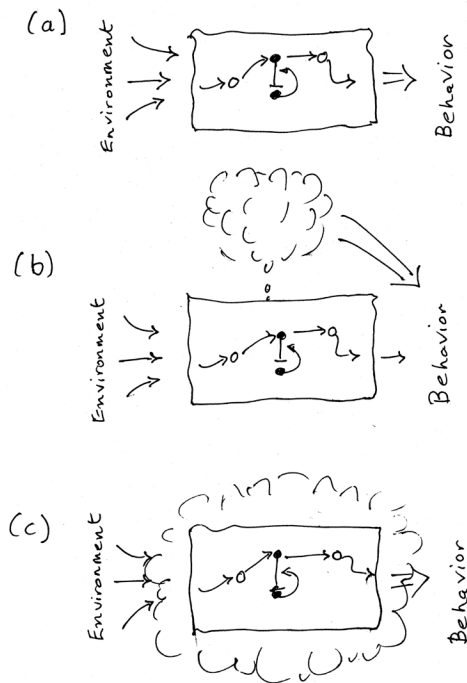
### ***Application and Anecdote***

Another writer, more industrious and better informed than I am, would be able to spell out how the ideas and findings of learning theorists—outlined above—can be applied to the phenomena studied under the heading of comparative cognition. I hope, therefore—given my inadequacies—that the readership of this journal, who will be fully informed about work in comparative psychology, will be able and willing to pursue such applications for themselves. My further hope is that this will help to bring about a union of work in comparative psychology and in learning theory; specifically, that the mechanisms identified by learning theorists might be shown to form the basis of, for example, spatial learning, concept formation, rule learning, and the rest. Having equated learning theory with the intensive study of a model system designed to reveal principles of general applicability, any learning theorist would be disappointed if it turned out that much of interest in psychology was not covered by these principles. To pursue the parallel offered in the introduction to this article, this would be like discovering that Mendel's laws turned out not to apply to the genetics of species other than the pea and the fruit fly.

The anecdote that follows (not to be taken too seriously) is intended to convey how my interpretation has been rejected by some, but how I hope it might all turn out all right in the end.

Some years ago we had a visit from a comparative psychologist interested in social interactions in primates. He gave a talk to the group that worked in my lab, the details of which I now forget; but it was concerned with the behavior of zoo-housed primates interacting over the availability of food. The issue was something such as, How did they interact when one could see another who could see the food available but was invisible to the first? The results were intriguing, discussion was vigorous, and soon it turned into a free-for-all in which the principles of learning theory were applied in order to derive an explanation of the behavior observed. (“How about: the context plus the presence of individual A serves as an occasion setter activating the inhibitory association formed by B between the food container and an approach response . . .,” etc., etc.) Quite soon the blackboard was covered with scribbles like those in Figure 1(a), where the box represents the animal and the symbols inside represent associative links and the like. While this was going on, I noticed that our visitor (who had remained silent) was looking disconcerted, and even distressed. When asked why, he replied that what we were offering was not the right sort of explanation at all.





**Figure 1.** Learning theory and cognition: Alternative interpretations

My response was to modify the blackboard drawing to look like Figure 1(b), saying (in jest), “Surely you don’t think it’s like this?” It was then my turn to be disconcerted when he responded, “Yes; that is just what I think.”

That was some time ago. If any of the present generation of comparative psychologists has the same view—that is, if they *define* their field as being beyond the reach of learning theory—then the bulk of this review is irrelevant to them. But there is reason to think that times have changed, and that learning theory and the study of comparative cognition are in the process of establishing a mutually beneficial relationship. It is significant that the primary journal covering learning theory changed its title in 2014 from *Journal of Experimental Psychology: Animal Behavior Processes* to *Journal of Experimental Psychology: Animal Learning and Cognition*. This has not been a change in name only; it fairly reflects the nature of the content. Consider the second issue of Volume 44, 2018. Of the eight experimental reports, three of them—contributed by authors who would probably acknowledge their training as learning theorists—are directly concerned with animal cognition (articles on category discrimination, on cognitive flexibility, and on attention in a multidimensional discrimination in pigeons). And the major report that starts the issue (Miller, 2018) not only uses the standard procedures for operant discrimination training in the pi-

geon to address questions about social learning but also makes use of associative learning theory (specifically, the Rescorla-Wagner model) in interpreting the results.

One noted student of comparative cognition, who has made major contributions to the field, has long been willing to acknowledge the effectiveness of so-called killjoy explanations for apparently complex instances of cognition (Shettleworth, 2010) and to argue that “complex behavior often arises from simple elements” (Shettleworth, 2012, p. 541). Encouraged by this, we may hope that the true state of affairs, when it comes to describing the social behavior of the primates of Figure 1, could turn out to be something like Figure 1(c). This is meant to represent the proposal (hinted at in what has gone before) that the cognitive processes, of interest to all psychologists, have their basis in the same set of mechanisms that determine the way in which the laboratory rat adjusts its behavior to cope with the demands of the experimental laboratory. The principles revealed by learning theory are thus not to be contrasted with the phenomena that constitute cognition; rather, they could form an explanation of the mechanisms responsible for it.

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