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General Process Learning Theory: Challenges from Response and Stimulus Factors

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Traditionally, general theories of learning have focused on associative and other mechanisms that are responsible for conditioned behavior without seriously considering how those mechanisms might vary depending on the stimulus being learned about and the response that provides evidence of learning. Recent studies of sexual conditioning in male domesticated quail have revealed both quantitative and qualitative variations in the functional properties of conditioned behavior depending on the response that is measured and the events or objects that serve as conditioned stimuli. For example, sexually conditioned sign tracking behavior is directly related to the ratio between context exposure (C) and trial duration (T) in a conditioning procedure, but sexually conditioned goal tracking is inversely related to the C/T ratio. Other studies have shown that conditioned stimuli that include limited cues from a female quail support different forms of sexually conditioned behavior than conditioned stimuli that lack female features. Furthermore, these various conditioned responses are differentially sensitive to extinction and reinforcer devaluation. The implications of these findings for general process learning theory are discussed.

Investigators have found the allure of general process theory to be irresistible since the inception of the study of learning. The first modern learning theorists, Thorndike and Pavlov, both examined learning in a variety of situations. Thorndike, for example, used 15 different puzzle boxes in his research, and Pavlov examined both appetitive and aversive conditioning. However, Thorndike and Pavlov were not interested in how the unique features of a particular situation produced unique forms of learning. Rather, they were interested in the commonalities of learning across situations.

Thorndike’s famous Law of Effect, for example, states that the presentation of a satisfying event (S*) after the performance of a response (R) results in an S-R association that connects the response to the stimuli (S) present when the response was made. Thorndike knew that some responses were resistant to instrumental reinforcement and introduced the concept of “belongingness” to describe these exceptions. However, qualifications to the Law of Effect were ignored by learning theorists for more than 50 years after the original statement of the principle.

All of the great learning theorists of the twentieth century focused on general mechanisms of learning that were stated in terms of abstract stimulus and response units. Hull, Tolman, Guthrie, and Estes all followed

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Thorndike’s and Pavlov’s lead in seeking to identify general principles that would account for learning irrespective of the stimuli or responses involved (Bower & Hilgard, 1981). The dogged pursuit of general mechanisms was also the basis for Skinner’s focus on the “arbitrary” operant. The arbitrary operant was supposed to be a form of behavior that was not dependent on the evolutionary history of the organism under study. Thus, the arbitrary operant was supposed to capture general rather than species specific features of behavior and learning. Encouraged by Skinner’s claims, investigators became comfortable with studying learning in a few “representative” situations, such as rats pressing a response lever and pigeons pecking a key light.

**Why the Emphasis on General Processes?**

A variety of factors have encouraged the emphasis on general processes in studies of learning in the twentieth century. Perhaps the most important of these is that a search for generality is simply good science. Science is not the cataloguing of isolated individual instances but the categorization and systematization of observations into general laws.

All major theories in science are general theories. Evolutionary theory, for example, seeks to characterize the factors that lead to changes in the prevalence of particular traits across generations, resulting in the appearance of new species and the disappearance of some old ones. The power of evolutionary theory is that it provides a general framework for systematizing the remarkable diversity of plant and animal life. The periodic table is another prominent example. The elements and compounds that exist in the world are not as numerous as the number of living species but the diversity is impressive. The periodic table serves to systematize this diversity by pointing out that the behavior of different elements can be predicted on the basis of their atomic weights.

General process learning theory is not as broadly conceived as evolutionary theory or the periodic table of the elements. Its goal is not to systematize diverse observations. Rather, it seeks to identify universal principles that operate in many different situations. Thus, it is more like Newton’s laws of motion or Boyle’s law stating the relation between the pressure and volume of a gas. These relationships or principles are assumed to be true for many different objects and gases. In a similar fashion, general process learning theory assumes that the principles of learning are true across a broad range of stimuli and responses. Learning theorists have followed in the footsteps of Darwin, Newton, and Boyle in formulating general principles.

The emphasis on general processes in the study of learning was also encouraged by the adoption of the model systems approach. Much of science operates by focusing on model systems. A model system is an experi-
mental preparation that is presumed to capture the critical features of the phenomenon of ultimate interest. Typically model systems are studied in place of a phenomenon in its real world context because of convenience and accessibility. For example, information about the mechanisms of the action of a drug in people might be obtained by studying how the drug works in an isolated tissue preparation, because the drug effect can be much more readily manipulated and measured in vitro rather than in vivo. The assumption that the model system behaves in the same way as the phenomenon of ultimate interest is based on an assumption of generality. Thus, a belief in general processes is a prerequisite for the use of model systems, and the use of model systems encourages adopting a general process theory.

Another source of the emphasis on general processes by major learning theorists was no doubt their sense of confidence and self-importance. For example, Thorndike formulated his Law of Effect based largely on his Ph.D. dissertation. Not many Ph.D. candidates have the self-confidence to characterize their findings as illustrative of a new and innovative “law.” One has to have a substantial measure of chutzpah to proclaim a general principle or law. Great scientists tend not to be humble and tentative in their declarations and are therefore not afraid to proclaim general principles.

**Challenges to General Process Learning Theory**

The general process view of learning was seriously called into question in the early 1970s by a number of books and review articles that highlighted various findings that appeared to challenge the generality of classical and instrumental conditioning (Hinde & Stevenson-Hinde, 1973; Rozin & Kalat, 1971; Seligman, 1970; Seligman & Hager, 1972; Shettleworth, 1972). These findings included the failure of positive reinforcement to increase the behavior of depositing a token into a slot (Breland & Breland, 1961), the ineffectiveness of punishment in suppressing certain types of responses (Walters & Glazer, 1971), limitations on the conditioning of various avoidance responses (Bolles, 1970), and selective associations in aversion learning (Garica & Koelling, 1966). These and other limitations on the effectiveness of classical and instrumental conditioning were thought to reflect the specialized adaptations of the organisms under study and were labeled “biological constraints on learning” (see Domjan, 1983, for a review).

Biological constraints on learning were the subject of heated debate during the 1970s and threatened to shake the foundations of learning theory, as investigators turned their attention to seemingly specialized forms of conditioning such as taste aversion learning (Barker, Best, & Domjan, 1977) and autoshaping or sign tracking (Hearst & Jenkins, 1974; Locurto, Terrace, & Gibbon, 1981). However, the threat to general process theory turned out to be short lived (Domjan & Galef, 1983). With few exceptions
(e.g., Domjan, 1994; Domjan, 1997; Timberlake & Lucas, 1989; Timberlake, 2000), investigators have returned to characterizing mechanisms of conditioned behavior in terms of generic models in which responses and stimuli are presumed to be interchangeable with one another (e.g., Gallistel & Gibbon, 2000; Dragoi & Staddon, 1999; Machado, 1997; Pearce 1994; see also Pearce & Bouton, 2000). However, ignoring the nature of the stimuli and responses involved in a learning experiment may be premature. In the remaining sections of this paper, I will review recent evidence from studies of sexual conditioning that indicates that the functional properties of conditioned behavior differ both quantitatively and qualitatively depending on the response that is measured and the stimuli that signal reinforcement.

**Quantitative Variations in Conditioned Responding as a Function of the Conditioned Behavior**

Laboratory studies of learning typically involve measuring just one aspect of behavior. Skinner, for example, advocated measuring the rate of lever pressing or key pecking. Investigators using a straight alley runway typically measure the speed of running in different portions of the alley. These and similarly limited response features are selected because they are reasonably easy to measure and because they are sensitive to the learning manipulations that are of interest. However, if only one behavior is measured, one cannot determine how the rules of conditioned behavior depend on the response itself.

In a recent study, Hilliard, Domjan, Nguyen, and Cusato (1998) established sexually conditioned behavior in male domesticated quail by presenting a three-dimensional object (the conditioned stimulus or CS) just before the males were given the opportunity to copulate with a female quail (the unconditioned stimulus or US). A somewhat unusual CS was used (see Figure 1). It consisted of a terry cloth object that included a taxidermically prepared female head. Such a CS object elicits little behavior unconditionally but quickly becomes associated with copulatory reinforcement (see Hilliard et al., 1998). The particular advantage of such a CS is that it can elicit a number of different conditioned responses. Copulatory behavior in male quail consists of the male grabbing the back of the female’s head, mounting on her back with both feet, and bringing its cloaca in contact with the female’s cloaca. When a CS object includes the cues of a female’s head, the grab, mount, and cloacal contact response sequence can also occur as conditioned behavior directed towards the CS (Cusato & Domjan, 1998). Another prominent conditioned response is CS-directed approach behavior.
Hilliard et al. (1998) examined the effects of sexual satiation and extinction on sexually conditioned behavior. All of the subjects first received 7 conditioning trials, which was sufficient to establish fairly vigorous conditioned approach, mount, and cloacal contact behavior. (Grab responses also occurred but were not systematically recorded.) The results of the sexual satiation experiment are summarized in Figure 2. Approach to the CS (top panel) was measured in terms of how much time the subject spent in a rectangular area (46 x 42 cm) in which the CS was located. The maximum score possible was 120 s. Mount and cloacal contact responses were measured in terms of the frequency occurrence using video tape records of the test trials. Satiation was accomplished by permitting the subjects to copulate with 0, 1, 4, or 8 females just before the test trial.

As Figure 2 shows, each of the conditioned responses declined with satiation. This outcome is the familiar US devaluation result that is obtained when the value of the reinforcer is reduced following conditioning (Holland & Rescorla, 1975; Holland & Straub, 1979). US devaluation effects are important because they imply that the conditioned behavior is mediated by stimulus-stimulus (S-S) rather than stimulus-response (S-R) mechanisms (Rescorla, 1973). The results in Figure 2 indicate that US devaluation effects occurred for all three measures of conditioned behavior. In addition, sexual satiation suppressed conditioned mount and cloacal contact responses much more than conditioned approach. Although conditioned
Figure 2. Mean seconds spent near the conditioned stimulus object (a), number of mounts (b), and number of cloacal contacts (c) during successive test blocks as a function of the number of females (0, 1, 4, or 8) that were introduced before each test to produce sexual satiation. (From Hilliard et al., 1998. Copyright 1998 by The Psychonomic Society, reprinted by permission.)

Figure 3. Mean seconds spent near the conditioned stimulus object (a), number of mounts (b), and number of cloacal contacts (c) as a function of trials (1-4) across eight extinction sessions. (From Hilliard et al., 1998. Copyright 1998 by The Psychonomic Society, reprinted by permission.)
approach declined with sexual satiation, even after access to 8 females, the
subjects approached the CS an average of about 30 s. In contrast, virtually
no conditioned mount and cloacal contact responses occurred after exposure
to 8 females.

One might suggest that the conditioned mount and cloacal contact re-
sponses might have declined faster than conditioned approach because the
mount and cloacal contact responses depended on first approaching the CS.
However, conditional probability analyses ruled out this interpretation.
These analyses showed that the declines in mount and cloacal contact re-
sponding were significantly greater than what was expected from the de-
creased opportunities brought about by the subjects spending less time near
the CS when they were sexually satiated (see Hilliard et al., 1998). Thus,
the results reflected a genuine difference in the susceptibility of the condi-
tioned approach and sexual contact responses to disruption by satiation.

A similar differential sensitivity of the approach, mount, and cloacal
contact responses was observed in the extinction experiment. The experi-
ment involved presenting four extinction trials (nonreinforced presentations
of the CS) each day for 8 days. This enabled Hilliard et al. to observe both
within-session and between-session extinction effects. The results are sum-
marized in Figure 3. Little systematic extinction occurred between sessions.
Decrements in behavior were more evident across the four extinction trials
conducted during each session. In addition, these decrements were much
more dramatic for the conditioned mount and cloacal contact responses than
for the approach response. Thus, as in the satiation experiment, the condi-
tioned mount and cloacal contact responses were more easily disrupted than
was conditioned approach. Conditional probability analyses showed that
these effects could not be attributed to changes in the opportunity to engage
in mounts and cloacal contacts as a function of within-session extinction
(see Hilliard et al., 1998).

The results presented in Figures 2 and 3 are unexpected from the per-
spective of classical ethology. Approach to a sexual conditioned stimulus is
analogous to what ethologists have referred to as appetitive behavior. In
contrast, mount and cloacal contact responses are more akin to consumma-
tory behavior, since they are involved in completing the copulatory re-
sponse sequence. Tinbergen (1951) characterized consummatory behavior
as more rigid and inflexible than appetitive behavior. However, in Hilliard
et al.’s experiments, the consummatory responses showed greater suscepti-
bility to satiation and extinction than the appetitive approach response. Hil-
liard et al. discussed various possible reasons for their results. For the pur-
poses of the present argument, the primary relevant conclusion is that the
functional properties of the conditioned responses depended on the nature
of the behaviors that were measured.
Qualitative Variations in Conditioned Responding and Stimulus Control as a Function of the Conditioned Behavior

The results of Hilliard et al. (1998) represent quantitative differences in the functional properties of various forms of conditioned behavior. The next example illustrates that qualitative differences in the functional properties of conditioned behavior can also be observed when different responses are measured. These observations were made by Burns and Domjan (2001) in the course of studies of the spatial properties of sexually conditioned behavior. Burns and Domjan used an arbitrary CS object (a block of wood lowered from the ceiling of the experimental chamber) in studies of sexual conditioning. The CS was presented 112 cm from the door that provided the male quail with the opportunity to copulate with a female. By separating the spatial location of the CS from the location of the female, Burns and Domjan were able to distinguish conditioned responses that consisted of approaching the location of the female (goal tracking) and conditioned responses that consisted of approaching the location of the CS (sign tracking).

The independent variable Burns and Domjan manipulated was the duration of the CS (trial time or T) relative to the duration that the subjects spent in the experimental context before the CS was presented on each conditioning trial (context time or C). The C/T ratio was selected for examination because previous studies with several species had shown that conditioned behavior is an increasing function of the C/T ratio. This increasing function had been obtained in studies of sign tracking in pigeons (Gibbon & Balsam, 1981) and studies of goal tracking in rats (Holland, 2000; Lattal, 1999; see also Gallistel & Gibbon, 2000). Burns and Domjan were interested in whether this relationship would be also obtained when both sign tracking and goal tracking were measured in the same experiment.

Using independent groups, Burns and Domjan tested C/T ratios of 1.5, 4.5, 45, and 180. In Experiment 1 the C/T ratios were created by keeping trial time constant and varying the context time. In Experiment 2, the same C/T ratios were created by keeping the context time constant and varying the trial time. Similar results were obtained regardless of which strategy was used. Therefore, only the results of the first experiment are presented here.

The sign tracking and goal tracking that developed during the course of the experiment are summarized in Figure 4. The top panel represents data obtained before the CS was presented, and the bottom panel represents data obtained during the CS. Focusing first on the CS-period data (bottom panel), it is evident that contrasting functional relations were obtained for the sign tracking and goal tracking response measures. Sign tracking increased with increasing C/T ratios, as is typically reported in the literature (Gallistel & Gibbon, 2000; Gibbon & Balsam, 1981; Holland, 2000; Lattal, 1999). However, goal tracking showed the opposite functional relation. The
greatest levels of goal tracking were evident with low C/T ratios, and increases in the C/T ratio produced decreases in goal tracking.

Another important finding concerned the stimulus control of the two forms of conditioned behavior. The extent to which responding was controlled by the CS can be evaluated by comparing responding during the CS (bottom panel) with responding during a comparable period before the CS was presented (top panel). This comparison shows that sign tracking was controlled primarily by the CS. The subjects did not approach the CS area until the CS was actually presented. In contrast, goal tracking was not controlled by the CS. Groups 1.5 and 4.5, which showed the highest levels of goal tracking during the CS also approached the goal area during the pre-CS

*Figure 4.* Conditioned sign tracking and goal tracking as a function of the C/T ratio during the pre-CS and CS periods. (Based on Burns & Domjan, 2001.)
period. In contrast, groups 45 and 180, which did not show goal tracking during the CS also did not show goal tracking during the pre-CS period.

The CS in this experiment was presented 112 cm from the goal area. Therefore, if subjects showed sign tracking and approached the CS, they could not at the same time approach the goal area. Accordingly, high levels of sign tracking were accompanied by low levels of goal tracking and vice versa (see Figure 4, bottom panel). However, response competition between sign tracking and goal tracking does not explain why one response predominated at low C/T ratios and the other predominated at high C/T ratios or the differences that were observed in the stimulus control of the two forms of conditioned behavior.

**Variations in Conditioned Responding as a Function of the Conditioned Stimulus**

The functional properties of conditioned behavior also vary as a function of the conditioned stimulus that is used. This conclusion is supported by studies that were designed to evaluate the impact of including the cues of a taxidermically prepared female head in a CS object. The experiments compared procedures in which the CS was a terry cloth object that included female cues (Figure 1) with procedures in which a similar terry cloth object served as the CS but with the female head cues replaced by additional terry cloth. The results indicated that including the cues of a female head on a CS object dramatically changes the results that are obtained.

The first obvious impact of including the cues of a female head on a CS object is that such a CS is much more likely to generate conditioned copulatory responses (grabs, mounts, and cloacal contact responses) than a CS that is made entirely of terry cloth. The results of one such study (Cusato & Domjan, 1998) are summarized in Figure 5. The subjects in this study received trials in which a CS object was presented either paired (P) or unpaired (U) with the opportunity to copulate with a female quail. As expected, CS–US pairings produced more responses directed towards the CS than was evident in the unpaired control groups. In addition, including cues of a female head in the CS object produced significantly more grab, mount, and cloacal contact responses. Interestingly, in this study the female head cues had little impact on conditioned approach to the CS object.

The findings of Cusato and Domjan (1998) are provocative but may reflect performance rather than learning effects. Perhaps female cues make a CS object more effective in supporting grab, mount, and cloacal contact responses, without substantially changing how such a CS enters into associations with the US. Although plausible, such a performance account is discouraged by other experimental results that employed blocking and second–order conditioning designs. Köksal, Domjan, and Weisman (1994) showed that a previously conditioned audiovisual cue successfully blocked
the conditioning of a CS object that was made entirely of terry cloth. However, the conditioned audiovisual cue was not successful in blocking the conditioning of a CS object that included female cues. More recently, Cusato and Domjan (2001) showed that a first–order CS that included female cues produced significantly more second order–conditioning than a first-order CS that was made entirely of terry cloth.

Further evidence of the effects of including female cues in a CS object was obtained in an extensive study by Akins (2000). Among other things, Akins was interested in the circumstances under which different forms of appetitive sexual behavior come to be established through Pavlovian conditioning. She examined the conditioning of general search behavior as contrasted with focal search behavior. Males looking for a female presumably begin with general search activities that are not directed at a particular location in space and then shift to focal search once they have identified where

*Figure 5.* Comparison of sexual conditioned responses to a CS object that either includes the cues of a female’s head and neck or lacks these species typical cues. The panels show mean time spent near the CS and mean frequency of grab, mount, and cloacal contact responses directed at the CS during nonreinforced test trials in groups that received the CS either paired (P) or unpaired (U) with sexual reinforcement. (Based on Cusato & Domjan, 1998. Copyright 1998 by Academic Press, reprinted by permission.)
the female may be found. Thus, general search behaviors are expected to predominate when there is a long delay before a female becomes available, and focal search should predominate when access to a female is more imminent (Timberlake, 2000). Consistent with this prediction, Akins, Domjan, and Gutiérrez (1994) previously found that focal search behavior developed when subjects receive sexual reinforcement 1 min after the onset of a CS. In contrast, general search behavior developed if sexual reinforcement was provided 20 min after CS onset.

Akins (2000) examined the short (1 min) and long (20 min) delay intervals in greater detail. The subjects were tested in a large experimental arena (183 cm x 61 cm) that provided ample opportunity for locomotor behavior. Focal search was defined as approaching and spending time near the conditioned stimulus. In contrast, general search was defined as pacing back and forth between one side of the experimental chamber and the other. Independent groups received the conditioned stimulus either for a short (1 min) or a long (20 min) duration before access to a female. For some groups the CS was made entirely of terrycloth (T) whereas for others it included the cues of a female’s head and neck (HN). Control groups received the short or long CS unpaired with access to a female.

The results are summarized in Figure 6. The top panel represents general search behavior, as measured by the frequency of crossing from one side of the apparatus to the other. The bottom panel represents focal search behavior, as measured by the percentage of time the subjects spent near the conditioned stimulus. Because there were eight groups in the experiment, Figure 6 is a bit confusing. However, consideration of the results is simplified if one notes that by the end of the experiment, none of the unpaired control groups showed much responding, regardless of whether general or focal search was measured.

The greatest level of general search behavior (Z1-Z2 crossings) occurred in subjects that received the terrycloth CS for a long duration (20 min) before access to a female (T-Long Paired). None of the other groups showed substantial general search behavior. In contrast, the greatest level of focal search behavior (% time in Zone 0) occurred in the two groups that received access to a female 1 min after the onset of the CS (T-Short Paired and HN-Short Paired). Increasing the duration of the CS from 1 min to 20 min resulted in a dramatic loss of focal search responding in subjects conditioned with the terrycloth CS (T-Short Paired vs. T-Long Paired). Increasing the duration of exposure to the head+neck CS also disrupted focal search behavior a bit. However, substantial levels of focal search continued to be evident in group HN-Long Paired.

The results displayed in Figure 6 clearly illustrate that functional relations obtained in Pavlovian conditioning depend a great deal on what stimulus serves as the CS and which behavior is measured as the conditioned response. When a terrycloth CS was used, an increase in the CS duration from
Figure 6. Mean frequency of locomotion from one side of the apparatus to the other (top panel) and time spent near the CS object (bottom panel). Independent groups received paired or unpaired presentations of a CS object with sexual reinforcement (the unconditioned stimulus or US). The CS-US interval (and duration) was either short (1 min) or long (20 min). The CS object either included the head and neck of a female (HN) or was made entirely of terrycloth (T). (From Akins, 2000. Copyright 2000 by Academic Press, reprinted by permission.)

1 min to 20 min eliminated focal search behavior but increased general search responding. However, both of these effects occurred only if the CS did not include cues of a female’s head and neck. With the head+neck CS,
substantial levels of general search were never obtained, and increasing the CS duration from 1 min to 20 min decreased focal search behavior only moderately. Thus, the head+neck CS elicited primarily focal search and this conditioned response was not very sensitive to the duration of the CS.

Some of the results obtained by Akins (2000) could reflect competition between different types of responses. One might argue, for example, that focal search is not possible if subjects are engaged in general search behavior. Therefore, a reciprocal relation should be evident between focal and general search. However, focusing on possible competition between responses is not helpful for two reasons. First, the data are not entirely consistent with such an interpretation. For example, it is unlikely that subjects conditioned with the head+neck CS failed to show general search behavior simply because they were engaged in focal search. Had that been the case, the decrease in focal search that occurred when the head+neck CS duration was extended to 20 min should have resulted in an increase in general search at the 20 min CS duration. But, that did not occur. A response competition account is also not helpful because it begs the question as to why one response predominates under certain circumstances and the other predominates under other circumstances. For example, the notion of response competition does not explain why increasing the CS duration from 1 min to 20 min resulted in a change from focal search to general search behavior for subjects conditioned with the no-head CS.

Implications for General Process Learning Theory

That evidence of learning depends on what response is measured and what event or object is used as the conditioned stimulus is not in itself challenging to general process learning theory. We all know that one cannot obtain evidence of learning unless one employs a sufficiently sensitive behavioral measure, and not all stimuli are equally effective in learning experiments. In fact, much of the unwritten laboratory lore in research on animal learning involves developing just the right response measures and finding just the right stimuli that will reveal the learning phenomena of interest (Timberlake, 2001a).

Response Sensitivity

Some of the evidence reviewed above can be “dismissed” on the grounds that it just illustrates differential sensitivity of certain responses and stimuli to conditioned modification. Consider, for example, the finding that consummatory sexual responses are more sensitive to satiation and extinction manipulations than conditioned approach behavior (Figures 2 and 3). Based on these results, one might conclude that consummatory responses provide more sensitive measures of learning. However, such a simple inter-
pretation is not consistent with all of the evidence described above. For example, this simple interpretation does not explain the differential functional relations that were observed by Burns and Domjan (Figure 4) between C/T ratios and sign tracking and goal tracking. The important issue raised by the Burns and Domjan data was not that sign tracking was a less sensitive measure of learning than goal tracking (or visa versa). Rather, the main point was these two responses were related to the C/T ratio in opposite ways. Thus, neither response measure could provide a complete or “true” account of the effects of the C/T ratio on conditioned behavior.

A simple response sensitivity hypothesis also cannot explain various aspects of the results obtained by Akins (2000). For example, an increase in the CS duration from 1 min to 20 min produced declines in focal search behavior with both of the CSs that were employed. However, that same increase in the CS duration produced an increase in conditioned general search behavior. It is difficult to argue that one of these response measures was generally more sensitive than the other.

The contrasting functional relations that were obtained with different measures of behavior in the present experiments have important implications for both the methods used to study animal learning and the theories that are used to explain the results. Methodologically, such findings indicate that measuring just one form of conditioned behavior is apt to provide an incomplete picture of learning at best and may in fact provide a misleading picture of what was learned in the experiment. This methodological implication has broad ramifications because most studies of learning report on only one type of behavior. One cannot help but wonder how our principles of learning would be altered by more comprehensive examinations of the behavioral consequences of learning.

The behavior that is measured to provide evidence of learning is rarely a critical part of our theories of learning. Theories are typically stated in terms of “associative strength” (e.g., Rescorla & Wagner, 1972) or response probability or rate (Machado, 1997), without concern for what activity is actually being measured. In fact, concerns about the behavioral manifestations of learning are often considered peripheral to, and less important than, concerns about learning. “Learning” is typically distinguished from “performance,” with the added implication that issues related to performance are less important and interesting than issues related to learning. The data reviewed here suggest that issues of performance cannot be divorced from issues of learning because the functional relations that characterize learning depend on what response is being measured.

Stimulus Salience or Intensity

General theories of learning have been a bit more generous when it comes to stimulus factors. However, even there, the accommodations have
been limited. Differences in learning as a function of the stimuli used are usually attributed to differences in stimulus salience or intensity (e.g., Rescorla & Wagner, 1972). To explain the above data in terms of stimulus salience or intensity, one has to assume that a CS object that contains the cues of a female head is more salient or intense than a no-head CS. With the added assumption that stronger conditioning is required to produce conditioned consummatory responses than conditioned appetitive behavior, one can explain many of the above findings.

The fact that including female cues in a CS facilitates the conditioning of copulatory responses (grabs, mounts, and cloacal contacts; Akins, 2000; Cusato & Domjan, 1998) is consistent with the idea that these responses require stronger conditioning and female head cues increase the salience of the CS. The salience account is also consistent with the finding that a female head CS is more effective in a second-order conditioning procedure (Cusato & Domjan, 2001) and is more resistant to blocking (Köksal et al., 1994) than a CS without female cues. However, the salience account fails to explain why the head CS was less effective in conditioning general search behavior than a no-head CS (Akins, 2000). Thus, a simple salience account is inadequate to explain the full range of findings.

**Towards a New General Process Learning Theory.**

Taken together, the present results suggest that general theories of learning are incomplete if they do not consider how the functional relations involving learning manipulations are modulated by both the behavior that is measured and the stimuli that serve in the experiment. Furthermore, response and stimulus factors are not likely to determine just the level or magnitude of learning effects, as is assumed by common general process theories. Rather, response and stimulus factors also determine the qualitative relationships between learning variables and behavioral outcomes.

A general theory of how response and stimulus variables determine the functional relations of learning remains to be worked out. We do not know enough about how learning variables interact with the preexisting organization of behavior to be able to predict or characterize with precision the behavioral outcomes of learning. The most valiant effort to integrate response and stimulus factors into a general theory of learning has been carried out by Timberlake (Timberlake, 2001b; Timberlake & Lucas, 1989). Timberlake’s behavior systems theory has been criticized because it lacks the quantitative precision of more traditional general process theories of learning. However, this lack of precision stems more from the limitations of the available corpus of data on learning than conceptual weaknesses of the theory. As more information becomes available on how learning is manifest in a variety of different behaviors and with a variety of different stimuli, we
should be in a better position to develop general theories of learning that incorporate response and stimulus factors more successfully.

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