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Conditioned Avoidance

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Summary. The procedure described here involves training an animal to make steady contact with a reward spout in order to receive food or water and then pairing a stimulus with mild electric shock delivered through the spout. The animal quickly learns to avoid the shock by breaking contact with the spout whenever it detects the stimulus. The breaking of contact with the spout is then used to indicate that the animal detected the stimulus. This procedure can be used to assess sensory and perceptual abilities in a wide variety of animals.

1 Introduction

In devising a psychophysical procedure for use with animals, it is important to choose a task which utilizes an animal's natural responses and is therefore easily learned. One response common to many animals is to freeze or suppress ongoing behavior when a stimulus that signals danger is detected. This suppression of behavior was experimentally investigated by Estes and Skinner in 1941, and has been used extensively by James C. Smith of Florida State University as a psychophysical procedure (Smith, 1970; Thaw & Smith, 1992). Referred to as *conditioned suppression*, it involves training an animal to make a response, such as pressing a lever to obtain food, and then presenting a stimulus followed by an electric shock. After a few stimulus-shock pairings an animal will cease responding when the stimulus is presented; this cessation of responding is then used to indicate that the animal detected the stimulus. It should be noted that this procedure is a *two-choice* task in which a subject makes one response in the presence of one stimulus and a different response when that stimulus is absent or a different stimulus is present.

Over the years, we have gradually modified the procedure developed by Smith in order to simplify training and accelerate testing. The procedure we now use represents a significant departure from the original conditioned suppression procedure in that it allows an animal either to avoid or escape the shock. Like conditioned suppression, this *conditioned avoidance* procedure has proved useful in testing the sensory and perceptual abilities of a wide variety of animals.

2 Conditioned Avoidance Procedure

The following is a description of the conditioned-avoidance procedure which has been developed in the course of the comparative study of mammalian hearing. Although most of the examples in this chapter have been drawn from that field, this procedure can be applied, *mutatis mutandis*, to any two-choice discrimination involving animals.

2.1 Overview of the Procedure

A hungry or thirsty animal is placed in a test cage and allowed to consume a steady trickle of food or water which is dispensed through a "reward" spout as long as the animal is in contact with the spout. Next, a suprathreshold stimulus is presented at random intervals and followed by a mild electric shock delivered through the reward spout. The animal soon learns to associate the stimulus with the shock and breaks contact with the spout whenever it detects the stimulus thereby avoiding the shock. The presentation of the stimulus constitutes a *warning* trial and breaking contact with the reward spout during a warning trial is taken as an indication that the animal detected the stimulus.

The response of an animal on each warning trial is recorded by a computer which determines whether or not the animal was in contact with the spout immediately before the shock was delivered. In signal detection terminology, breaking contact during a warning trial is referred to as a *hit*, while failure to do so is a *miss*. Because an animal occasionally breaks contact in the absence of a warning stimulus, its *false alarm* rate is obtained by determining its response rate during *safe* trials, that is, intervals when a stimulus could have been, but was not, presented.

A detection threshold is determined by reducing the intensity of the stimulus in successive blocks of trials until the animal no longer responds to the stimulus above the level expected by chance—in other words, the response rate during the warning trials no longer differs statistically from that during the safe trials. Similarly, a difference threshold is determined by reducing the difference between two stimuli until performance falls to chance. Threshold is defined as the stimulus level (or difference) resulting in a performance level of 50%.

2.2 The Test Cage

The design of the test cage is determined by the requirements of the stimulus as well as the species being tested. In auditory research where an animal is placed within a sound field, the cage is constructed of a sound-transparent material, such as wire mesh, and obstructions to sound are minimized (Fig. 1). An important feature of the test cage is the reward spout.

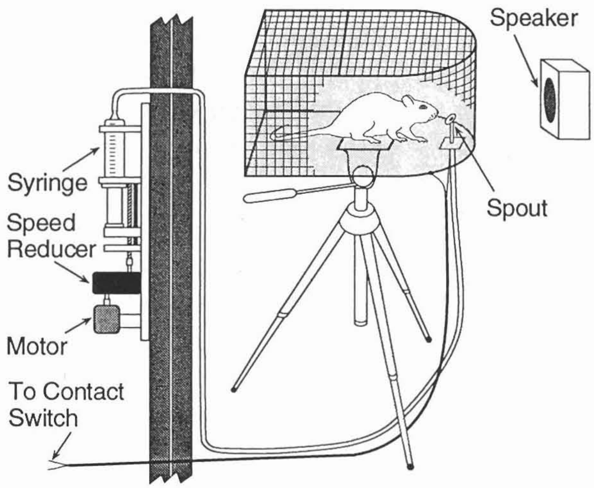

Figure 1. Semi-schematic drawing of a test cage and syringe pump.

Because the animal maintains contact with the spout, it can be used to position the animal precisely within the cage. In auditory testing, a reward spout which comes up through the bottom of the cage is preferred because it minimizes obstructions between the loudspeaker and the animal's ears. The spout can be made of copper or stainless-steel tubing with a small lick plate mounted on the top at an angle of approximately a 45°. The exact configuration of the spout depends on the species being tested—the goal is to construct a spout that requires an animal to hold its head in the desired position when making contact with the spout. In some cases, an animal may try to turn sideways while licking the spout, as when attending to sounds coming from one side. One way to prevent this is by placing shoulder-high wire mesh barriers within the cage to require the animal to face directly forward while licking the spout.

An animal's contact with the reward spout is detected with a contact switch connected between the spout and the cage floor (Fig. 1). Some animals, such as rabbits and least weasels, have fur on their feet which prevents them from making good electrical contact with the floor. This problem can be solved by wetting their feet or placing a damp sponge on the cage floor.

Larger animals, such as horses and other hoofed mammals, can be tested in a stall using a stainless steel bowl as a reward spout (Heffner and Heffner, 1984a). Contact with the reward bowl is detected by a contact switch connected between the bowl and a metal plate on the stall floor or an electrode taped to the animal's flank.

Primates are often tested in primate chairs, in which case the reward spout is mounted on the chair in front of the animal. One configuration consists of two drink tubes mounted parallel and close enough (1 cm apart) so that a monkey can comfortably place its mouth on both spouts. The spouts are electrically isolated from each other so that a contact switch can be used to detect when the animal places its mouth on them and the shock can be delivered between them. A reward, such as water, is delivered through either one or both of the drink tubes and auditory stimuli may be presented via insertion earphones or loudspeakers (Heffner and Heffner, 1990a).

The use of a reward spout to fix an animal's head may be helpful in testing other modalities, such as vision and olfaction, where placement of the head is important, as well as in somatosensory testing of the face or vibrissae (e.g., Hutson and Masterton, 1986; Smith, 1970). The range of tests depends primarily on the ingenuity of the experimenter: taste can be tested by injecting flavors into a water reward; somatosensory tests of a foot pad can be done by requiring an animal to place its foot on a stimulator in order to turn on the reward.

2.3 The Reward

The purpose of the appetitive reward is to keep an animal in continuous contact with the reward spout, breaking contact only when a warning stimulus is presented. To do this, it is necessary to use a reward for which an animal will reliably work and which can be delivered continuously or in many small amounts. For most mammals, the ideal reward is water, although in some cases a food puree or paste is preferable. The issues here are the type of reward, how to deliver it, and how to deprive an animal.

a) Water Reward

Water is an ideal reward for this procedure because most mammals readily work for it and, unlike food pellets, it can be continuously dispensed. An inexpensive way of delivering water is to use a constant-pressure water reservoir that is connected via an electrically operated water valve to the reward spout. The water reservoir can be a graduated cylinder with an outlet at the bottom. The cylinder is capped with a rubber stopper with an air inlet tube passing through the stopper to below the water level (see Heffner et al, 1994). The water pressure remains constant as long as the bottom of the air inlet tube is submerged; the water height is measured from the bottom of the air inlet tube. The water flow rate is controlled by first adjusting the height of the reservoir and then operating the water valve with a train of electrical pulses (e.g., 50 msec duration) that can be continuously varied (e.g., 2 to 8 pulses/sec) to provide fine control.

A drawback of the water reservoir/electric valve delivery system is that it can be difficult to dispense small amounts accurately, especially when an animal consumes 5 ml or less per session. In addition, the height of the water reservoir in relation to the reward spout must be kept constant and the reservoir height must be readjusted if the cage height is changed. A solution to this problem is to use a syringe pump and adjust the flow rate by varying its speed (Fig. 1). Although commercially-available syringe pumps are relatively expensive, it is possible to construct a satisfactory syringe pump in a modestly equipped shop (Thompson et al., 1990).

b) Food Reward

There are some animals for which food is the preferred reward. In general, these are animals that normally obtain most or all of their water from their food. They include desert rodents, such kangaroos rats and gerbils, which obtain metabolic water from dry food (Schmidt-Nielsen, 1979), and underground rodents, such as gophers and mole rats, which obtain water from the roots they consume. Because these animals cannot easily be deprived of water without also depriving them of food, a solution is to use a food paste or puree which can be continuously dispensed. Examples for rodents are strained vegetable or fruit baby food, and applesauce mixed with peanut butter. These diets can then be supplemented as needed with dry food (Heffner and Heffner, 1992, 1993). Animals whose diets consist primarily of insects may also work better for food. An example is the big brown bat (*Eptesicus fuscus*), which is typically maintained in the laboratory on a diet of mealworms. In this case, a food paste can be made of blended and strained mealworms, with cottage cheese added to obtain a uniform consistency. Finally, although water can be used to reward domestic cats, provided they are maintained on dry cat food (e.g., Masterton et al., 1994), cats are highly motivated by meat and often work better for meat paste. Although commercial baby food has been used (Berkley et al., 1971; Thompson et al., 1990), a more economical reward is canned cat food blended with water or milk and baby cereal to achieve the desired consistency.

Food pastes can be dispensed with a syringe pump (Thompson et al., 1990). The food should be carefully blended to eliminate lumps and clogging and the pump should be located directly beneath the test cage to minimize tubing length. For auditory testing, this necessitates the selection of a relatively quiet pump motor so as not to mask the auditory stimulus. Alternatively, a hydraulic system may be constructed in which the drive sits outside the test room and powers a piston which depresses the plunger of a food syringe located below the test cage.

c) Deprivation

In order to train an animal using an appetitive reward, it is necessary to remove the animal's food or water from its home cage and have it obtain its daily ration in the test cage. Although some animals may be trained to work for special treats, their performance breaks down when the discrimination becomes difficult (e.g., around threshold). The same may hold true for animals routinely given free access to the reward following a test session. Thus, data obtained under such situations may be suspect on the grounds that the animals were insufficiently motivated.

The usual procedure is to place an animal on deprivation and begin training the following day. The animal's body weight is recorded daily prior to testing and serves as a useful indication of its deprivational state. The animal is placed in the test cage and accustomed to maintaining steady contact with the spout. The reward rate is adjusted so that the animal works long enough to allow sufficient data to be collected and receives adequate reward to maintain a stable body weight. In rare instances, a species may not maintain its weight in a single daily feeding and can either be tested twice daily or else given supplements. Most animals can be trained to work steadily for about an hour, although some small animals that consume little may work for less time. Avoidance training is begun as soon as an animal is reliably maintaining steady contact, usually within one to three sessions.

The body weight at which an animal works well is usually between 80 and 90% of ad lib weight, although this depends on the species. For some species, an individual's weight must be reduced to well below 80% before it is sufficiently motivated (Heffner and Heffner, 1992), while others will work at or near 100% ad lib weight once they have adapted to the testing regimen (e.g., chinchillas). The goal is to keep an animal's weight as high as possible while maintaining sufficient motivation. An animal which is too hungry or thirsty may fail to respond to the warning stimulus until it has consumed enough to reduce its hunger or thirst. With experience, one can determine both an animal's optimal working weight and the amount of reward it needs to maintain that weight.

There are two important effects of deprivation on the health and well-being of an animal. First, animals living in the wild rarely have continuous access to food and water and by the standards applied to laboratory animals would be considered deprived. For example, wild pigeons brought into the laboratory and placed on ad lib feeding gained 9 to 30% body weight even though they had been trapped amid abundant food supplies (Poling et al., 1990). Furthermore, young guinea pigs placed on food deprivation for a behavioral study showed the same growth curves as guinea pigs living in the wild (Petersen et al., 1977). Thus, animals whose food or water intake is restricted in order to motivate them to perform in behavioral experiments appear to be operating at deprivation levels to which they are naturally adapted.

Second, there is a large literature documenting the fact that reducing the caloric intake of laboratory animals by 30 to 70% of ad lib feeding results in animals that are significantly healthier and longer lived than those on free feed. Specifically, dietary restriction greatly decreases the incidence and severity of degenerative diseases, retards the onset of tumors and reduces their incidence, and increases both lifespan and life expectancy (Bucci, 1992). Thus, restricting the food or water intake of animals not only reduces their weights to those of normal wild animals, but results in healthier animals.

Finally, it should be noted that although one may encounter the belief that water deprivation is more stressful than food deprivation (Orlans, 1991), there is little evidence to support this contention. Those wishing to study this issue should consult the article by Desimone et al. (1992).

2.4 Electric Shock

The purpose of the electric shock is to make the animal break contact with the reward spout whenever it detects a warning stimulus. Unlike conditioned suppression, the shock is avoidable, a feature which increases the number of warning trials that can be given in a session. Because the shock is avoidable, it is presented simultaneously with a signal, such as a light or buzzer, which indicates that the shock is on and provides feedback for successful avoidance.

The shock is adjusted to the lowest level that produces reliable avoidance. Too low a level results in a low hit rate and underestimates an animal's ability; too high a level results in a high false alarm rate which may make the data unusable. Ideally, the shock level is adjusted to give a false alarm rate of 1 to 10%, although false alarm rates as high as 20% can give usable data if the proper correction is applied (see below). The shock level is initially adjusted for each animal by presenting warning trials with the shock level set near or at zero voltage and rapidly increasing the level until the animal breaks contact with the spout when it senses the shock. The level can be gradually increased further until it is sufficiently aversive to cause the animal to break contact when it detects the warning stimulus. The shock level should be occasionally increased or decreased during testing to insure that it is at optimal level.

An important factor which allows the use a relatively low level of shock is the fact that an animal is required to break contact with the spout for a very brief interval (e.g., the last 200 msec of the trial, Fig. 2A). In contrast, the original conditioned suppression procedure required an animal to stop responding for 10 or more seconds (Ray, 1970; Smith, 1970). Because the cost to the animal of making a response is the temporary loss of access to the reinforcer, the shorter the required response time, the lower the level of shock needed. Moreover, the response cost to the animal can be compensated for by momentarily increasing the reward rate following a successful avoidance to make up for the small loss of reward (i.e., rewarding hits).

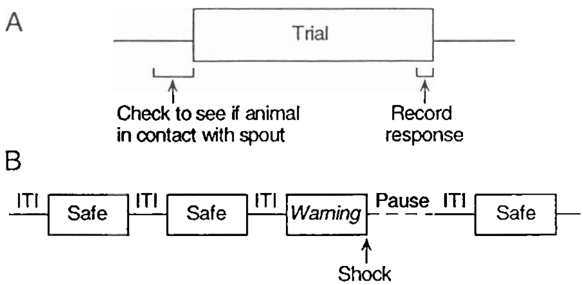

Figure 2. A: Schematic representation of a trial. B: Schematic representation of a trial sequence with the warning signal occurring on trial 3. Trial presentation is paused following a warning trial until the animal returns to the reward spout. ITI, inter-trial-interval.

The electric shock is a high voltage, low current stimulus, the level of which depends on the species and the degree of contact which the animal makes between the reward spout and cage floor. As a result, it is rarely helpful to specify the voltage and current settings; the preferred method is to specify the shock in terms of its behavioral effect on the animal. In general, small animals require lower levels of shock than larger animals. The shock duration is usually set between 100 and 300 msec. However, unlike conditioned suppression, the shock is escapable and the duration an animal experiences the shock is dependent on its reaction time and is generally well under 100 msec. Occasionally, an animal breaks contact when the warning stimulus is presented but returns to the spout before the trial has ended; this behavior can be eliminated by temporarily increasing the duration of the shock to 1 sec or longer.

There are several advantages to shocking the animals through the spout. Not only does it makes it easier for them to learn to break contact, but the sensitivity of the lips and tongue make it possible to use much lower levels than if they were shocked between their feet. In addition, the construction of the test cage is simplified because a grid floor is not needed. In the case of monkeys tested in a primate chair, the shock is delivered between the two water spouts.

The electric shock can be produced by a generator designed for behavioral research. Alternatively, a satisfactory shocker can be devised by using an inexpensive AC fence charger and controlling the shock level by adjusting the input voltage with a variable transformer.

With regard to the subjective sensation of the shock, it may be noted that electric shock is not a natural stimulus and while it can be quite aversive, its sensation is not adequately described as painful. For illustrative purposes, a helpful comparison is the neuromuscular stimulator commonly used on humans for physiotherapy. Tests in our laboratory with squirrels have demonstrated that such stimulators can serve as an adequate, if expensive, shock source (e.g., Medtronic, model 3128). Thus, the shock levels used with animals are typically within the range of those experienced by humans in therapeutic situations. Moreover, because the animals do not develop a fear of the reward spout and readily return to it after receiving a shock, the shock level is properly described as mild.

2.5 Trial Presentation

The test procedure consists of presenting a series of trials which ends either with the presentation of a warning trial (Fig. 2B) or after a fixed number of safe trials has been presented, i.e., a "sham" trial sequence. The duration of a trial, the inter-trial-interval (ITI), and the maximum number of trials in a sequence can be varied to suit the requirements of the particular test. For example, a trial can be 3-sec long, with an ITI of 2 sec, and the warning trial occurring from 1 to 7 trials after the last warning trial. In addition, a pause can be inserted after a warning trial to give an animal time to return to the spout or, alternatively, the testing sequence can be halted until the animal has resumed contact with the spout. Once an animal has resumed contact, a warning trial may be presented within 2 to 30 sec—or longer as sham sequences are occasionally inserted to prevent an animal from automatically responding after 30 sec.

It is important to distribute the warning trials so that each position in a sequence (i.e., positions 1 through 7 of the preceding example) has the same probability of containing a warning signal. If one randomly presents the same number of warning trials in each trial position, the probability of a warning trial will increase with position number. Thus, it is necessary to construct a "look-up" table in which the number of times a warning trial can occur in a particular position in the sequence is adjusted so that each position has approximately the same probability of containing a warning trial (Table I). This table can be used to construct a fixed sequence of safe and warning trials which is then repeated, rather than selecting the trials randomly. This is done to prevent an animal from receiving too many identical sequences in a row, especially sham sequences and sequences in which the first trial is a warning trial; sequences containing more than 80 warning trials are unlikely to be memorized by an animal. Typically, a sequence does not contain more than 3 warning trials in a row.

Table I. Look-up table for sequences from 1 to 7 trials long with overall probability of a warning trial equal to .221.

Position of Warning Trial in the Sequence	Number of Warning Trials in that Position	Number of Safe Trials in that Position	Probability of a Warning Trial
1st	10	36	.217
2nd	8	28	.222
3rd	6	22	.214
4th	5	17	.227
5th	4	13	.235
6th	3	10	.231
7th	2	8	.200
Sham*	8		

*A sequence of 7 safe trials not followed by a warning trial.

Our procedure for determining the ability of an animal to detect or discriminate a stimulus consists of presenting a particular stimulus value (e.g., a specific intensity) in blocks of 6 or more warning trials (for a titration procedure, see Masterton et al., 1994). Thresholds are initially estimated by gradually reducing the level of the stimulus until performance falls to chance. Next, detailed testing is conducted by presenting trials at levels just above, at, and below the estimated threshold. Typically, a block of trials involving a difficult discrimination is followed by a block of easier trials to ensure that an animal is still under control of the stimulus. However, it is occasionally necessary to continue a difficult discrimination in order to train an animal to "attend," as is the case when an animal must learn to listen for sounds near threshold.

The response of an animal is typically determined by measuring spout contact during the 200 msec preceding the shock and recording a response if the animal breaks contact for at least half of that 200-msec interval (Fig. 2A). The hit and false alarm rates are recorded separately for each block of trials as the false alarm rate often varies, increasing when the discrimination becomes more difficult and decreasing when it is easy. Because an animal may temporarily cease responding for other reasons (e.g., to groom), the results of a trial are automatically discarded if the animal is not in contact with the spout immediately preceding a trial (e.g., during the preceding .5 sec, Fig. 2A). Because this criterion is applied equally to safe and warning trials, it does not bias the results.

2.6 Data Analysis

The performance of an animal for a particular stimulus value is calculated by correcting the hit rate for the false alarm rate. The classic method for this is the formula: Performance = (Hit rate - False Alarm Rate)/(1-False Alarm Rate) (Green and Swets, 1966; Smith, 1970). However, this correction can give misleading results when high hit rates are accompanied by high false alarm rates. This is illustrated by the extreme case in which a perfect hit rate, 1.0, is accompanied by a false alarm rate of .99, a situation which results in the same perfect score of 1.0 as a hit rate of 1.0 and a false alarm rate of 0.

To better correct for the effect of false alarms, the following formula may be used: Performance = Hit Rate - (Hit Rate * False Alarm Rate). This calculation yields scores from 0 (failure to detect or discriminate) to 1.0 (perfect detection or discrimination without any false alarms). Unlike the classic method, a score of 1.0 can result only from a hit rate of 1.0 and a false alarm rate of 0. In practice, the scores resulting from this formula rarely reach 1.0 because it is desirable to keep the false alarm rate greater than zero to ensure that the animal is sufficiently attentive. Similarly, a score of 0 is usually not reached because an animal unable to detect or discriminate the stimulus will, on average, have a hit rate equal to its false alarm rate, which can give a performance score as high as .25 (i.e., hit and false alarm rates both equal to

.50). Because this formula works well for a wide range of hit and false alarm rates, it is the preferred formula. A detailed comparison of this formula with other measures can be found in Heffner and Heffner, 1988.

Threshold is defined as the stimulus value yielding a performance of .50, which is derived by interpolating if necessary. However, it is important to reduce the stimulus value to a level at which performance falls to statistical chance ($p > 0.01$) in order to rule out the possibility that an animal is using some other cue to perform the discrimination. For example, a sound localization task in which an animal is required to discriminate the locus of two loudspeakers can be confounded if an animal learns to distinguish the speakers by the quality of their sound. Thus, the angle of separation between the speakers must be reduced until performance falls to chance in order to demonstrate that the animal is indeed discriminating locus.

The probability of a particular score can be determined using the binomial distribution (Hays, 1963). This is done using the formula:

$$p(X \geq r) = \sum_{x=r}^{N} \binom{N}{r} p^r q^{N-r} \qquad (1)$$

This formula gives the probability of observing a hit rate, X, equal to or greater than the observed hit rate, r, where N is the number of warning trials, p is the false alarm rate, and q is the *correct rejection* rate, i.e., 1-False Alarms. The result is the probability of obtaining a hit rate equal or greater than that observed, given the observed false alarm rate for that stimulus level.

3 Discussion

The following points can be made regarding the conditioned avoidance procedure. First, the basic training and conditioning can be accomplished in a relatively short time. Because licking is a natural response, mammals typically require no special training to maintain steady contact with the reward spout. Furthermore, once an animal is acclimated to the testing situation, it can be trained within the first session to break contact reliably when an easily detectable or discriminable warning stimulus is presented. As with all procedures, training an animal to attend carefully to stimuli near threshold requires additional practice.

Second, the results obtained with conditioned avoidance have been shown to be highly replicable. Not only is there less variation between subjects than often found when using a purely positive reward procedure (e.g., Heffner and Heffner, 1984a), but comparisons between data obtained by different laboratories show good agreement (cf., Heffner et al., 1994; Kelly and Masterton, 1977).

Third, this procedure can be applied to a wide variety of animals and tests. It has been used with over 30 species of mammals, as well as birds, to assess sensory, perceptual, and cognitive abilities in any test involving two choices (e.g., Heffner & Heffner, 1990b, Smith, 1970). Not only is it an ideal procedure for difficult to test animals (Heffner & Heffner, 1984a), but unlike simple fear conditioning (LeDoux et al, 1984), it works well with animals brain damaged in a wide variety of ways (Heffner & Heffner, 1984b; Kelly & Judge, 1985).

Fourth, conditioned avoidance does not appear to result in "experimental neurosis," a condition which refers to the development of long-standing behavioral disturbances in animals in certain test situations (e.g., Deese, 1958). These disturbances, which include struggling on the part of the animal during testing, have been observed in conditioning experiments involving positive reward, as well as shock, and may appear when an animal is subjected to lengthy testing on a difficult discrimination. The fact that such behavior has not been observed in conditioned avoidance may be due to the fact that the animal can terminate the experiment at any time by failing to return to the reward spout. As a result, an animal cannot be subjected to prolonged unwarned shocks (as when the stimulus is below threshold) beyond its capacity to tolerate them.

Finally, as noted by Smith (1970), a procedure that combines aversive control with positive reinforcement gives good control over an animal's performance (i.e., its hit and false alarm rates). Too low a hit rate can be corrected by increasing the shock level while too high a false alarm rate can be corrected by reducing the shock level and/or increasing the rate at which the reward is delivered. In this way, an animal's behavior can be adjusted to yield its best performance. A procedure which relies solely on positive reward, on the other hand, may lack sufficient punishment for errors. Such procedures usually rely on an "error-time-out" in which testing is momentarily halted following a miss or false alarm. However, the temporary lack of opportunity to obtain access to a reward is not always sufficient punishment for errors and some animals will not perform at optimal levels in a positive reward procedure, especially when the discrimination becomes difficult. While this is not always the case, it should be kept in mind when the results of such tests yield variable or unusually poor performance.

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