

findings remains to be established, it is obvious from the results presented here that dominant male mice have a distinct social advantage over subordinate male mice since they assiduously label their environment with an excretory product that has a demonstrated capacity to elicit profound behavioral and physiological effects on the reproductive processes of females (2, 3).

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4. Under the conditions described, mouse urine fluoresces a bright blue. Preputialectomized males show the same pattern of blue-fluorescing marks. In addition, we found that mice receiving a single intraperitoneal injection of 0.25 ml of a 1 percent solution of methylene blue, Sudan black, or basic fuchsin produced urinary marking patterns that were indicative of the dye injected and similar to those that we observed under ultraviolet light.
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6. The filter paper containing radioactivity associated with [3 H]inulin was cut into 1-cm squares and extracted five times, each time with 100 ml of water at 70°C for 15 minutes, with constant mixing. Successive extracts were pooled, and an aliquot (1 ml) was removed and placed in a scintillation vial with 10 ml of Insta-Gel (Packard Instrument Company). The scintillation vials were dark-adapted and cooled to 10°C before counting. In all cases sufficient radioactivity was allowed to accumulate to give a probable error of 2 percent or less. We corrected all radioactivity determinations to 100 percent efficiency (expressed in disintegrations per minute) by counting each sample against a ^{226}Ra external standard and comparing the value obtained to a standard correlation curve (count rate of the external standard versus the percent efficiency of samples of known radioactivity containing varying amounts of a quenching additive). Preliminary experiments demonstrated that the extraction procedure described above was adequate to recover 98 ± 1.5 percent of the radioactivity associated with chromatographically pure [3 H]inulin.
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Errorless Discrimination, Autoshaping, and Conditioned Inhibition

Abstract. Pigeons were exposed to a discriminated autoshaping procedure in which brief presentation of a green light on a key was always followed by food whereas presentation of a vertical white line on the key was never followed by food. Pigeons acquired an errorless discrimination by pecking reliably in the presence of the green light but never in the presence of the line. The line inhibited pecking in later tests; when the white line was paired with food, key peck acquisition was retarded; and when the white line was superimposed on the green background, responding was suppressed.

Discrimination learning is a process through which the environment comes to control an organism's behavior. In a discrimination, an organism's behavior is reinforced in the presence of one stimulus (S+) but is not reinforced in the presence of another stimulus (S-). As a result, the organism comes to respond to S+ but not to S-. Of central importance to the understanding of discrimination learning is an analysis of the origin of nonresponding to S-. Terrace (1) has argued that there are two fundamentally different types of discrimination learning, which are distinguished primarily by how nonresponding to S- comes about. In the first type, the organism responds to S- (that is, he makes "errors") during discrimination learning, and responding to S- is eventually inhibited. An organism that learns with errors presumably learns two things: to respond to S+ and not to respond to S-. In the second type, the organism learns without errors, and S- does not come to inhibit responding. Supposedly, an organism that learns without errors learns only to respond to

S+. Thus, Terrace contends that nonresponding to S- results from inhibition by S- only if errors occur during learning. The purpose of this report is to determine whether an errorless S- may become inhibitory.

Before environmental stimuli acquire control over a skeletal response such as the pecking response of a pigeon, the pigeon often makes many errors (1). Terrace demonstrated, however, that the occurrence of errors is not necessary for discrimination learning. He trained pigeons to discriminate without errors between red and green lights. Having begun discrimination training soon after conditioning of the key peck, he initially made S- very different from S+. At first, S- was less bright, of shorter duration, and of different hue than S+. During training, he progressively increased the brightness and duration of S- so that S+ and S- differed only in hue. This method for producing errorless learning is called a fading procedure.

Whether discrimination learning occurs with or without errors, the organism finally responds to S+ but not to S-. However, there are important differences in the behaviors observed during acquisition of a discrimination with and without errors. For example, Terrace argues that when learning with errors occurs, the pigeon emits emotional responses to S-, the S- becomes aversive, and peak shift, behavioral contrast, and inhibitory stimulus control occur (1). These features are called "by-products" of discrimination learning (1). These by-products are absent if the learning was errorless.

Terrace (1) contends that the absence of by-products after errorless learning indicates that an errorless S- is not inhibitory. But testing for the presence of discrimination by-products is not the most direct method of determining whether S- is inhibitory (2). For example, if S- is a conditioned inhibitor, then, as a result of learning, it

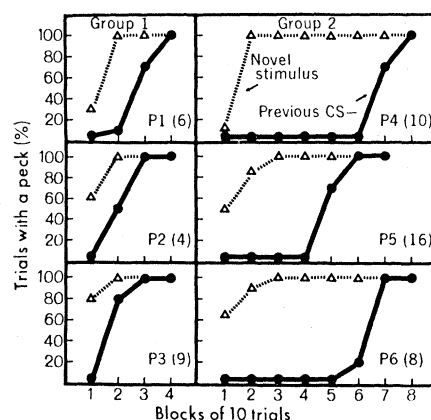


Fig. 1. Mean percentage of trials during which at least one peck occurred for successive blocks of ten trials in the retardation test. Each graph shows data for one bird (identified by P plus number), and the total number of errors made by each is shown in parentheses.

should suppress responding when presented simultaneously with another stimulus that controls a high level of responding. Also, it should be difficult to train an animal to respond to an S— that had previously acquired inhibitory properties. In previous errorless learning experiments (1, 3), the latter types of test for the inhibitory properties of S— were not included.

In the present experiment, errorless learning was produced in food-deprived pigeons by presenting a green light that was always followed by food (response-independent pairing) and a white vertical line that was never paired with food (explicit nonpairing). This procedure, a type of discriminated autoshaping procedure, will hereafter be called differential conditioning. In autoshaping, differential light-food pairings produce conditioning of the pigeon's key peck (4, 5), while explicit nonpairings do not (4). A differential conditioning procedure rather than the fading procedure was used to assess the inhibitory nature of an errorless S— by a procedure other than Terrace's. If errors are necessary for the establishment of S— as a conditioned inhibitor, then an errorless S— from any procedure should not be an inhibitor.

Twelve experimentally naive white Carneaux pigeons maintained at 80 percent of their free-feeding weight were studied. All events in a standard, two-key Lehigh Valley experimental chamber were monitored by electromechanical equipment. A houselight constantly illuminated the chamber. Stimuli were provided by display cells (Industrial Electronics Engineers) mounted directly behind the key.

Before the start of the experiment, each bird was trained to approach and eat readily from the standard food hopper containing mixed grains. Food was delivered independently of behavior, and the duration of food presentation was progressively decreased from 15 to 4 seconds and remained at 4 seconds for the entire experiment. After food hopper training, the pigeons were divided randomly into four groups, and experimental sessions began.

The two phases of the experiment for each group are shown in Table 1. Group 1 received 160 differential conditioning trials in phase 1. Each session consisted of 80 trials. On 40 of these, a green light (CS+) was presented on the left key for 6 seconds and was followed immediately by food. On the remaining 40 trials, a white vertical line

Table 1. The conditions of the two experimental phases for each group; DC, differential conditioning; RT, retardation test; CCT, combined cues test.

Group	Phase 1	Phase 2
1	160 DC trials	RT
2	400 DC trials	RT
3	400 DC trials	CCT
4	200 CS+ trials	CCT

on a black background (CS—) appeared on the left key for 6 seconds but was never paired with food. Trial order was random except that neither type occurred more than three times successively. The left key was darkened for a variable time between trials, which averaged 30 seconds. All presentations of stimuli and food were independent of the animal's behavior. In phase 2, group 1 received a retardation test designed to assess the difficulty of conditioning the bird to peck at the white line. The test consisted of pairing either CS— or a novel stimulus with food. The novel stimulus was used to see whether the effects of differential conditioning were specific to the CS—. Each session consisted of 20 presentations of CS— on the left key and 20 presentations of a novel stimulus, a white light, on the right key. Each stimulus lasted 6 seconds and was followed by food. Stimuli were presented successively in random order; as before, the mean intertrial interval was 30 seconds.

Group 2 was given 400 differential conditioning trials, more than twice as many as group 1, so that the difficulty of conditioning the key peck to CS— could be related to the number of non-

pairings of CS— with food. For this group, phase 1 consisted of five 80-trial sessions of differential conditioning identical to those for group 1, and phase 2 was a retardation test identical to that for group 1.

For group 3, phase 1 was identical to that for group 2. In phase 2, group 3 was given two combined-cues tests for the suppressive effects of the white line. The combined-cues tests were given in successive sessions in which the birds never received food. Each session consisted of 15 presentations of a test stimulus—the white line on a green background—that was a combination of CS— and CS+. The test stimulus was always presented on the left key. The average intertrial interval was 30 seconds.

Group 4 was a control for the unconditioned suppressive effects of the white line. In order to demonstrate that any suppressive effect of CS— for group 3 was the result of conditioning, it was necessary to show that the white line did not as strongly suppress the ongoing responding of birds that had never received explicit nonpairings of line and food. For group 4, phase 1 consisted of 200 CS+ trials, 40 trials per session, with a mean intertrial interval of 60 seconds. Groups 3 and 4 thus received the same number and average frequency of CS+ trials during phase 1. During phase 2, group 4 received two combined-cues tests identical to those for group 3. A small suppressive effect of the white line for group 4 would be expected because of generalization decrement or novelty (2).

During phase 1, the CS+ acquired control of key pecking within 90 trials for all birds. No bird in groups 1, 2, or 3 emitted more than 16 responses to CS— for all CS— trials during phase 1. The performance of all birds (median errors, 8; range, 4 to 16) was "errorless" by Terrace's criterion of no more than 25 errors (1). The median number of intertrial pecks was 6 (range, 0 to 13). There were no systematic differences in intertrial responding between groups.

Figure 1 shows the results of the retardation test for groups 1 and 2. For each bird in group 2, acquisition of key pecking to the white line occurred after at least twice the number of pairings required for any bird in group 1. Therefore, the difficulty of conditioning the key peck to the white line was dependent on the number of

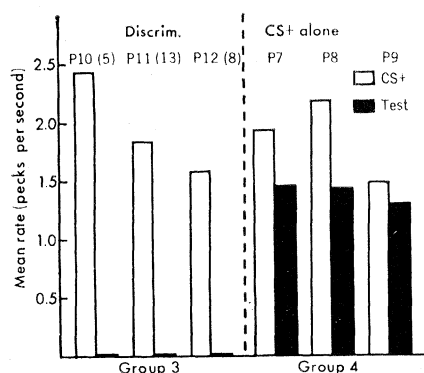


Fig. 2. Mean response rate on CS+ trials and on combined-cues test trials for each bird in group 3 (Discrim.) and group 4 (CS+ alone). Group 3 had received differential conditioning trials in phase 1, while group 4 had received an equal number of only CS+ trials.

nonpairings of line and food from phase 1. More nonpairings resulted in slower acquisition of pecking to the white line. For each bird, key peck acquisition occurred within 20 trials for the novel stimulus. Since the acquisition rate for the novel stimulus was unrelated to the amount of differential conditioning, the retardation effect was specific to CS—.

Figure 2 shows the results of the combined-cues tests for groups 3 and 4. The mean response rates to the test stimulus are shown in comparison to the mean rates for the same number of randomly selected CS+ trials from the last session of phase 1. Similar response rates were controlled by CS+ in groups 3 and 4. Relative to CS+, the test stimulus totally suppressed responding for each bird in group 3. In contrast, the response rate to the test stimulus was similar to that of CS+ alone for group 4. The slight suppression of responding by the white line for group 4 could be due to generalization decrement. The results of the combined-cues tests show that the suppressive effect of the line for group 3 was due to conditioning factors.

The results of the retardation test together with those of the combined-cues tests show that an errorless S— can inhibit responding. Therefore, the occurrence of errors is not necessary for the establishment of S— as a conditioned inhibitor. These results strongly support the view that nonresponding to S— in errorless discrimination learning can result from inhibition by S—.

Since nonresponding to S— can result from inhibition by S— in learning with and without errors, the environment may not control behavior in qualitatively different ways in the two cases. A major problem for future study is whether similar environmental events produce discrimination learning with and without errors. Specifically, the role of such ubiquitous factors in discrimination training as the differential association of stimuli with reinforcement and nonreinforcement should be investigated. Comprehensive analyses of the behaviors that may be conditioned by such events (6) will be fundamental to the analysis of how the environment acquires control over an organism's behavior.

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Chimpanzee Spatial Memory Organization

Abstract. *Juvenile chimpanzees, carried around an outdoor field and shown up to 18 randomly placed hidden foods, remembered most of these hiding places and the type of food that was in each. Their search pattern approximated an optimum routing, and they rarely rechecked a place they had already emptied of food.*

This report describes the performance of young chimpanzees in a delayed response variation on the "traveling salesman" combinatorial problem (1, 2). In other applied sciences this problem is: Given the positions of several places on a scaled map, find the routing that will take you to all of these places with the shortest mileage. Here, the problem is: If a chimpanzee has in the past seen the locations of several hidden objects in a field, how does he manage to get to them again, and how does he organize his travel route? What does his itinerary tell us about the nature of his "cognitive mapping," his strategy, and his criteria of "efficiency" (3, 4)?

Six wild-born chimpanzees, 5 to 7 years old, were tested in the outdoor enclosure (30.5 by 122 m) in which they had lived as a group for more than a year. Their previous formal test experience (5) did not include delayed response tests involving multiple hidden goals; one animal (Bido) had had fewer than ten prior trials of any delayed response testing.

Before a trial began, all six animals were locked in a release cage on the periphery of the field. Then one experimenter took out a previously selected test animal and carried him about the field, accompanying a second experimenter who hid one piece of fruit in each of 18 randomly selected sectors of the field. Throughout this 10-minute process, the animal was not permitted to do anything other than cling to his carrier and watch the baiter; thus, primary reinforcement and locomotor practice during the information-gathering phase of a trial were eliminated (6).

After being shown the foods, the

chimpanzee was returned to the group. The experimenters left the field, ascended an observation tower, and, within 2 minutes, pulled a cable that opened the release cage door. All six animals were released simultaneously and were free to roam. The five animals who had not been shown the food on a particular trial had no way to find the food other than through guesswork or cues such as odor, the behavior of the test animal, and inadvertent cues from the experimenters; thus, they served as controls for factors other than visual memory. The emotional dependence of the animals on each other precluded the possibility of testing each animal alone.

On a map that showed the location of each piece of food, the experimenters recorded the time at which each food pile was found or rechecked, and the identity of the animal involved. In addition, qualitative notes were made on behavior related to the search. Observation continued for at least 1 hour.

One trial was given each day for 16 days. Belle, Bandit, Bido, and Gigi each served as test animals on 4 trials and as control animals on the remaining 12 trials. Shadow and Polly were controls on all trials. On each trial the experimenters followed a different path and used a different set of 18 hiding places (7).

The animal that had been shown the food found a total of 200 pieces (12.5 per trial); the animals serving as controls found a total of 17 (0.21 per animal per trial). Usually, the test animal ran unerringly and in a direct line to the exact clump of grass or leaves, tree stump, or hole in the ground where a hidden food lay, grabbed the