Discrimination reversal learning in newts

STUART R. ELLINS, ROBERT E. CRAMER, and GLENN C. MARTIN
California State College, San Bernardino, San Bernardino, California

The results of field research suggest that, contrary to being behaviorally inflexible, some amphibians may have the ability to respond effectively to changing environments. The performance of seven newts (*Triturus viridescens*) was studied across 20 successive reversals of a spatial discrimination problem in a dry T-maze. Submersion in shaded water served as reinforcement for correct responses. The subjects showed a decrease in mean errors across reversals and across ordinal trials within sessions. These results are discussed in terms of the importance of using biologically relevant methodologies in the study of comparative animal learning.

Amphibians have the reputation of being difficult animals to train (Thorpe, 1963) and, according to Hodos and Campbell (1969), are behaviorally inflexible. This reputation, we believe, has contributed to a paucity of research on amphibian learning. Research using anurans constitutes most of the work conducted to date, and the results are, at best, mixed (e.g., Karplus, Algom, & Samuel, 1981; Thompson & Boice, 1975). The few studies that have used urodeles have also shed little light on our understanding of amphibian learning. Although Segal, Hershkowitz, Samuel, and Bitterman (1971), who used a shock stimulus, were successful in reducing the number of ascents by Spanish newts to the water surface, Ray (1967, 1970) found that tiger salamanders were unable to avoid an electric shock. Ray did report, however, that performance improved steadily when a bright light was used as an aversive unconditioned stimulus.

Hershkowitz and Samuel (1973) were able to train crested newt larvae in an appetitive discrimination task and reported that the training was retained by the adults after metamorphosis. However, only two of seven naive adults could be trained to criterion on the same discrimination task. Seidman (1949) reported that newts did evidence some error reduction across discrimination reversals, but a methodological flaw makes any conclusions equivocal, and, as a result, the research is largely ignored in the contemporary comparative learning literature.

In a series of field studies investigating homing orientation, newts successfully located their home area under a variety of displacement conditions (Twitty, 1959; Twitty, Grant, & Anderson, 1964, 1967). The results of subsequent research suggested that olfaction may play an important role in initial

homing orientation (Grant, Anderson, & Twitty, 1968). A sizable number of anosmic newts also manifested a correct initial homing orientation that suggested that the subjects were able to discriminate other nonolfactory cues. In addition, Landreth and Ferguson (1967) reported that experimentally blinded animals were successful in orienting toward their home area.

The results of research reported above suggest that, at least in some cases, it is possible to train urodeles, and permit the speculation that, contrary to being behaviorally inflexible, urodeles are capable of responding effectively to situational idiosyncracies. It is our contention that, to investigate urodele performance under laboratory conditions, one must use biologically relevant methodologies. All too often, arbitrary laboratory paradigms are used and the integral relationship between methodology and species-specific behavior is ignored.

It has been our experience that newts, like other urodeles, are difficult to train. Using conventional appetitive learning tasks, we have noted that they are generally lethargic and unresponsive to environmental stimulation. However, we believe that the homing orientation research suggests that newts are capable of responding effectively to a changing environment and that a task involving a series of discriminations may provide a mechanism for investigating naturally occurring behavior. In the homing research, newts returned to their home area only after having made a correct spatial discrimination, either upstream or downstream. Many of the newts were able to perform this task in spite of impaired olfactory or visual systems, which suggested that they can take advantage of a variety of information. In the present experiment, we examined the ability of newts to reduce errors across a series of successive discrimination reversals (SDRs). We chose SDR training because it has proved to be successful for studying a wide variety of divergent species (e.g.,

The authors' mailing address is: Department of Psychology, California State College, San Bernardino, San Bernardino, California 92407.

Bitterman, 1966; Ellins & Masterson, 1971; Gossette, 1966; Gossette & Hombach, 1969) and because studies of representatives of the class Amphibia are conspicuously absent from this literature.

METHOD

Subjects

The subjects were eight adult newts, *Triturus viridescens*, obtained from a local supplier. One newt died early in training, and no results for it are included in the data. The subjects averaged 10.0 cm in length. They were fed a daily ration of tubifex worms. They were housed in a 57-liter water-filled glass tank, which contained a wooden float to allow them to periodically climb out of the water. Throughout the experiment, the daily water temperature ranged from 19.5° to 24.5°C and the air temperature ranged from 19.0° to 25.5°C. Room lighting was provided by overhead fluorescent bulbs, which were on each day from approximately 8:00 a.m. to 11:00 p.m.

Experimental Paradigm

Although Seidman's (1949) results are at best equivocal, the basic paradigm, with some modification, provides a useful framework for investigating newt spatial discrimination learning. Seidman used a dry T-maze, with submersion in a container of shaded water serving as the reinforcer for a correct response; a cardboard barrier, visible from the choice point, was used to block access to the reinforcement in the event of an incorrect response. In the present experiment, the cardboard barrier was replaced by a nonvisible perforated false floor located just above the shaded water. This modification addressed two potential problems involving nonspatial cues: the use of the false floor controlled for the possibility that the solid cardboard barrier could serve as a visual discrimination cue, and the perforated false floor, unlike the solid cardboard barrier, would not be expected to attenuate possible olfactory cues and any moisture gradient emanating from the water in the negative arm of the T-maze. This modification controlled for the possibility that the subject could perform the discrimination by following differential olfactory and/or moisture cues.

Apparatus

The apparatus comprised a T-maze with 7.5-cm-high wooden walls and a black Plexiglas floor (see Figure 1). A black Plexiglas guillotine door separated the startbox from the arms of the T-maze and both arms from each other. The door was held up with an electromagnet and could be dropped by the press of a button. In the back of the startbox was a baffle that could be manually moved forward and backward. The baffle could be used to prod the animal to leave the startbox at the beginning of each trial.

The arms of the T-maze were 19 cm long and 9 cm wide. The hinged floors of the arms were also held up by electromagnets. A response line crossed each arm 11 cm from the guillotine door. In each arm there was a photocell, 14 cm from the guillotine door. When the photobeam was broken, the floor of that arm dropped. Under the floor of the arm designated "positive" was a white plastic container 12 × 12 × 10 cm deep, which was filled with 5 cm of water and gravel taken each day from the home tank. Under the floor of the arm designated "negative" was an identical container; placed within that container was a perforated false floor. The surface of the false floor was 2 cm above the floor of the container. Hence the water in the container, also from the home tank, was below the false floor. A lamp with a 60-W 120-V Sylvania incandescent bulb was positioned 45 cm above the floor of the apparatus at the choice point. Light illuminated the entire inside of the apparatus.

Procedure

All subjects were run on consecutive days in the late afternoon and early evening during the winter and spring. Subjects were run

Figure 1. T-maze drawn to scale.

in a random order each day. They were initially given 14 consecutive ¼-h daily pretraining sessions. In each session, a subject was required to run from the startbox to the end of either arm of the T-maze. If the subject did not leave the startbox within 3 min, it was gently prodded from behind with the baffle until it did. If the subject left the startbox but did not cross the response line within 5 min, the trial was reinitiated. When the subject left the startbox and its nose crossed the response line, the guillotine door was dropped to prevent its leaving that arm. When the subject proceeded down one of the arms and broke the photobeam, the floor of that arm dropped, which deposited the subject in one of the containers. The subject remained in the container, which held 5 cm of water, for 3 min. It was then lifted with a fish net and placed on a dry paper towel for approximately 15 sec to allow partial drying and then was replaced in the startbox. After each trial, the floor of the entire T-maze was thoroughly wiped dry with a paper towel.

The procedure used was identical to that used during pretraining, except that the container under one of the arms contained the dry perforated false floor. Each subject received 10 trials/day until a criterion of 8 of 10 correct responses to the positive arm was reached on a given day.¹ On the original discrimination problem, the right arm was positive for Subjects 1, 2, 3, and 4 and the left arm was positive for Subjects 5, 6, and 7. Each time a subject reached criterion, the positions of the wet and dry containers were reversed. Training was stopped after each subject reached criterion on 20 successive reversal problems.

RESULTS

After leaving the startbox, the subjects typically meandered to the choice point and then went either right or left. At the choice point, the subjects occasionally engaged in what appeared to be vicarious trial and error. At the completion of a trial, the response was noted as either correct or incorrect. The reduction of mean errors both across reversals and with daily sessions was analyzed. Figure 2 indicates a peak mean error score on the first reversal, followed by a gradual reduction in errors. An analysis of variance on reversals 1-20, with reversals as a re-

Figure 2. Mean errors on the original discrimination (OD) and on each of the 20 reversal problems.

Figure 3. Mean errors per ordinal trial position within sessions for blocks of reversals.

peated measure, revealed a significant reduction in errors [$F(19,114) = 2.47, p < .01$].

Figure 3 shows the distribution of mean errors across the 10 ordinal trials within sessions for blocks of reversals. A two-factor analysis of variance with ordinal trials as a repeated measure revealed a significant difference between reversal blocks [$F(3,240) = 36.30, p < .001$]. The results of a Newman-Keuls multiple-comparison procedure showed that significantly more errors occurred in reversals 1-5 than in reversals 6-10, 11-15, and 16-20 ($p < .01$). The latter three reversal blocks did not differ significantly. Neither the trials effect nor the interaction between blocks or reversals and trials was significant.

In order to examine the distribution of errors across trials within sessions, the data from all blocks of reversals in Figure 3 were collapsed. A single repeated measures analysis of variance revealed a significant effect for error reduction across trials [$F(9,240) = 3.33, p < .001$].

DISCUSSION

The pattern of error reduction depicted in Figure 2, involving a substantial error peak following the original discrimination and a subsequent reduction of errors across reversals, is consistent with the results of previously conducted SDR research with a variety of animals (e.g., Ellins & Masterson, 1971; Gossette, 1966; Gossette & Homback, 1969). The finding that newts are also capable of significantly reducing errors across ordinal trials (see Figure 3) is consistent with results from research using birds and monkeys (Gossette & Cohen, 1966; Gossette, Gossette, & Inman, 1966; Gossette & Inman, 1966). It is therefore apparent that, like that of other animals, the behavior of newts is not inflexible and that past difficulties in training may be a result of a failure to employ biologically relevant methodologies.

As indicated by Seligman (1970), organisms, on the basis of their unique evolutionary histories, bring specialized sensory-motor and associative neural equipment into experimental situations, which predisposes them to associate certain events more readily than others. For example, although Ray's (1967) tiger salamanders could not learn a one-way avoidance to electric shock, rapid learning did result when a bright light was used as the unconditioned stimulus. In the present study, the bright light above the apparatus apparently initiated escape movements, and submersion in the shaded water served as reinforcement for correct responses at the choice point. Submersion in the water reduced the newts' discomfort due to evaporative water loss and dry skin (Deyrup, 1964). This is consistent with field reports that indicate that, upon release, newts frequently appeared to be seeking escape or shelter from the conditions of the release site. Rather than orienting immediately to the home area, many of the newts sought relief from desiccation (Grant et al., 1968).

A considerable number of newts successfully oriented toward their home area in spite of impairment of selected sensory systems (Grant et al., 1968; Landreth & Ferguson, 1967). In the present experiment, newts successfully reduced errors when visual apparatus cues and olfactory cues emanating from the water were controlled. In addition, we thoroughly wiped the floor of the T-maze after each trial, thereby diffusing odor trails that may have been deposited by the newts throughout the apparatus. It is possible that the newts learned to perform the spatial discrimination on the basis of kinesthetic cues alone, but it is more likely that they responded to a variety of presently unknown and uncontrolled cues. In any case, these cumulative results suggest that newts may profit from a variety of information and are capable of responding effectively to a complex and changing environment.

On the basis of the present results, it can now be concluded that improvement across successive

discrimination reversals occurs in representatives of all vertebrate classes. Although various theoretical arguments concerning the nature of SDR learning remain (Bitterman, 1975; Gossette, 1969), differences in learning ability undoubtedly exist across animals. In the past these differences have been analyzed in terms of dichotomous categories such as "ratlike" and "fishlike" (Bitterman, 1965). Furthermore, it was argued that continuity in phyletic development could be based upon quantitative differences in learning ability on a given task. As Hodos and Campbell (1969) so adroitly pointed out, both of these approaches incorrectly assume the existence of a "phylogenetic scale," with all species under study representing a common evolutionary lineage. This notion is incompatible with the model of divergent evolution. We believe differences in performance on learning tasks are better understood in terms of the relationship between methodology and species-specific behavior. Perhaps by modeling biologically relevant procedures from the appropriate field research literature, learning in any animal can be thoroughly investigated.

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NOTE

1. To examine the effects of prodding on discrimination learning, a chi-square analysis was conducted on the training data. The results indicated that correct and incorrect responses were equally distributed across prod and no-prod trials [$\chi^2(1) < 1$]. Twenty-seven percent of the training trials were reinitiated. This evidence for behavioral passivity is consistent with previous findings in our laboratory and work in natural settings (see Grant et al., 1969).

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