Title
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LEARNING DURING EXPLORATION: THE ROLE OF BEHAVIORAL TOPOGRAPHY DURING EXPLORATION IN DETERMINING SUBSEQUENT ADAPTIVE BEHAVIOR

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ABSTRACT: Two investigations examine the hypothesis that one function of exploration is to create situations in which there is an opportunity to acquire useful information. In the first, male rats (*Rattus norvegicus,* Sprague-Dawley strain) with enriched (EC) or impoverished (IC) experience (leading to differences in exploratory behavior documented previously) were given an opportunity to explore an arena with a hidden escape route on two consecutive days. On the following day, subjects were chased by a mechanical device and the time required to escape the arena was recorded. No group differences were seen in pre-chase behaviors other than those related to the hidden escape route, or in stress-related behaviors while being chased. EC rats escaped significantly more quickly than IC rats, and a composite score derived from pre-challenge behavior in the arena was correlated significantly with escape time under challenge. In the second experiment, EC and IC subjects were chased without previous experience in the area; EC rats escaped significantly more quickly than IC rats. In an analysis of the combined results from the two experiments, both environmental history and pre-challenge arena experience were found to exert significant influence on escape time. These findings demonstrate that different behaviors *during* exploration can lead to functionally significant differences in the information acquired *as a result* of exploration.

Much of the experimental investigation of learning hinges upon studies involving animals under the constraint of having to perform a task which has been imposed by the investigator. Most of animal learning outside of the laboratory, however, is necessarily the product of events that occur during spontaneous activity. Exploratory behavior seems likely as one of the behavioral phenomena through which such learning can take place.

Spontaneous exploratory behavior, outside the context of foraging (e.g., in satiated animals), has been a subject of interest for many years. Both Small (1899) and Slonaker (1912) mentioned behaviors that were apparently inquisitive, and more recently several others have investi-

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gated and offered explanations for exploration (e.g., Berlyne, 1950 et seq.; Glanzer, 1958; Welker, 1961). The typical operational definition, however, has equated spatial locomotion with exploratory behavior (for an exception, see Glickman and Sroges, 1966); measures of locomotion in some variant of the open field test are the primary behavioral variable used in most studies. Although it is widely used, the open field situation has serious defects as a data-gathering technique for the measurement of voluntary behavior. Primary among these defects is the substantial confusion over exactly what is being measured in this test. At the very least, there can be little doubt that behavior in the typical open field test is determined by multiple factors. Considerable evidence exists that measures of locomotion may in fact be measures of the subject's attempt to escape the open field (see, for example, Suarez & Gallup, 1981 and Welker, 1957; the report of Hayes, 1961, occasionally cited as a rejoinder to Welker, 1957, seems not to address the same issues). If an animal is attempting to escape the open field, this implies a motivational state not consistent with behavior patterns under unstressed conditions; it is difficult to attribute cognitive significance to locomotor behavior in such a situation.

In addition to the methodological inadequacy of the open-field test, moving about in empty space is not equivalent to situations most likely to be encountered by animals outside the laboratory. Animals engage in a variety of behaviors while exploring, and many of these behaviors are involved with investigation of specific features of the environment, e.g., objects. Less, however, is known about the nature of object investigation during exploration.

It has previously been shown that exploratory behavior in the laboratory rat *(Rattus norvegicus)* shows experience-dependent changes and that spatial locomotion and object interaction are separable entities. Renner and Rosenzweig (1986) found that adolescent rats with a relatively enriched experience history (designated EC, for enriched condition) showed higher levels of behavioral complexity during interaction with objects than littermates with a relatively impoverished experience history (designated IC, for impoverished condition). These changes occurred without concurrent changes in locomotion or amount of object contact. In adults, changes in exploration appear in both behavioral complexity of object investigation and on several measures of overall quantity of exploration (Renner, 1987).

Although few straightforward empirical investigations have been reported concerning the function of exploration, many hypotheses have been advanced. Welker (1961) states that "learning invariably occurs in any situation that evokes exploration" (p. 201). Some type of hypothesis that exploration might be a part of animal information-processing has

been a common theme, offered also by Glickman and Sroges (1966) and more recently by Toates (1983). The data upon which these speculations are based are, however, often incomplete or indirect.

There is evidence for learning during spontaneous activity, but closer scrutiny reveals it to be learning only about spatial locations, and this learning depends only minimally on the subject's behavior. This evidence dates back to the latent learning studies of Blodgett (1929) and Tolman and Honzik (1930), wherein subjects formed cognitive maps of spatial arrangements without the incentive of experimentally-provided reward. Albert & Mah (1972) extended these findings by establishing that animals can subsequently show memory for the location of an already-relevant stimulus discovered through locomotor activity. These are, however, essentially questions of spatial learning. Furthermore, procedures in these studies were designed so that even random locomotion would have exposed the subject to the information to be learned. Exploration, if it is viewed as functionally meaningful, cannot reasonably be treated as the animal equivalent of Brownian motion.

The purpose of the studies reported in this paper was to find out whether behavioral topography determines what is learned during exploration. Specifically, this investigation is designed to examine the proposition that the specific behaviors displayed during exploration, as well as their organization, contribute to determining the type of information obtained as a result of exploring, and to present evidence relevant to that hypothesis.

In a previous study (Renner, 1987), adult rats with a relatively enriched experiential history showed a different behavioral organization than their experientially impoverished littermates. In this experiment, the clearest environmentally-induced difference in the specific behaviors of adult rats was in the category of climbing: adult rats previously housed in enriched conditions climbed more on large objects than littermates previously housed in impoverished conditions. As a consequence of this behavioral difference between rats with enriched and impoverished experience, there may be differences in the information available to the subjects with different histories; i.e., it is possible that these experientially-induced differences in climbing behavior could in some circumstances lead to changes in the amount and/or type of information acquired about the environment during exploration. The resulting difference in knowledge of the environment could, in turn, be significant under conditions of environmental challenge (e.g., predation). This may be a useful model for study of possible benefits of information acquisition via exploration. This report concerns two studies of the consequences of an environmentally-induced alteration in exploratory behavior for rats' ability to behave adaptively under the challenge of simulated predation.

EXPERIMENT I
Method

Animals

Sixteen male Sprague-Dawley rats, group-housed in standard colony conditions until the beginning of the experiment, were studied. At 90 days of age, the rats were divided into weight-matched pairs and were placed into either enriched (EC) or impoverished (IC) conditions.

Environmental Conditions

Environmental conditions were identical to those described fully by Bennett and Rosenzweig (1981), and so will be described only briefly here. The enriched condition consisted of housing in a group of 12 (including additional filler rats to complete the group) in a large cage (75 x 75 x 40 cm) containing various stimulus objects. Objects were selected from a collection of items kept in the laboratory, including tunnels, wooden playthings, metal enclosures, and junk objects; approximately half of these objects were replaced daily with others from the collection. This procedure provided daily opportunities for investigation of novel objects and novel arrangements of both familiar and unfamiliar objects. In the impoverished condition (IC) each animal was housed singly in a small hanging cage with solid stainless steel sides and mesh floor and front panel. All rats had access to food and water a libitum. Rats in both groups were handled equally and were housed in the same room as the experimental apparatus was located. The room was lighted from 0700-1900 daily.

Apparatus

Tests were carried out in a wooden arena with an available area 120 cm square, surrounded by Plexiglas walls 60 cm high. A round hole 10 cm in diameter was cut in the center of the arena floor, leading to a plastic tub cage (with a layer of wood shavings on its bottom) on a shelf suspended from the underside of the arena floor. The wooden surfaces of the arena were painted medium gray. Black paint lines 1 cm wide divided the floor of the arena into a grid of nine equal-area zones. A wooden box (30 x 40 x 13 cm high) was placed in the center of the arena over the escape hole. A 10 cm hole was centered in the top of the box, and a piece of corrugated cardboard was wedged in the interior of the box to provide a ramp to the arena floor inside the box. This ramp divided the 30 cm drop from the top of the box to the bottom of the tub cage into three steps. The height of this obstruction box had been determined through pilot testing, ensuring that all subjects were capable of easily climbing an

object of this size. A radio-controlled mechanical model car (Nikko RDC 24120, slightly larger than the rats) was used for the simulation of environmental challenge by predation. The model emitted a high-pitched motor noise while it was in motion.

The arena was illuminated by two 25w red bulbs, which were clamped at opposite corners on top of the Plexiglas wall. Dim general room illumination was provided by a single 25w white bulb in a metal shade oriented toward a wall of the testing room, approximately 2 m from the arena; the lamp was positioned so that there was a gap of approximately 3 cm between the metal shade and the wall.

All procedures were recorded on videotape. A low-light video camera was placed in the room for observation of the arena. All additional equipment was in an adjacent room, in order to eliminate the possibility that equipment noise could affect the rats' behavior. The signal from the video camera was passed through a character generator (Panasonic WJ810), which superimposed the current time and date, as well as elapsed time within each session, on a selected portion of the video image. This composite signal was routed to a videotape recorder (Panasonic NV8950). Additional details of the videotaping procedure may be found in Renner & Rosenzweig (1986).

Procedure

After 30 days of differential housing, subjects were moved to holding cages labelled with code numbers such that the tester was blind as to previous housing condition. All testing was carried out under dim red illumination during the first few hours of real-time evening (which was early in the dark phase of the subjects' daily light-dark cycle). The cage rack holding all animals was wheeled to an adjoining room for the duration of each test session to control for possible intrusive effects from olfactory or auditory stimuli. On each of two consecutive nights, each rat's individual cage was carried into the test area and the subject was placed in the arena for 10 minutes. On the first two nights, two novel stimulus objects (chosen from a pool of junk objects kept in the laboratory) were placed in the arena along with the obstruction box described above. The same objects in the same locations were used for a particular subject on both nights. Objects were replaced approximately every fifth subject. Object location was also varied nonsystematically across subjects. Although urine and feces were removed from the arena between tests, the arena was not cleaned with any solvent during the experiment.

On the third night, under lighting conditions identical to those of the first two nights, subjects were individually tested in the arena. Stimulus objects other than the obstruction box were removed from the arena floor prior to introduction of the subject, and a fiberboard box with

paper end curtains was centered against one wall of the arena. After the subject had spent three minutes in the arena a simulated predator (the radio-controlled car described above) emerged from this box; the car was controlled by the experimenter from the next room to chase the subject (without making contact) for 180 seconds or until the subject escaped into the obstruction box.

Although the remote operator attempted to make the model approach the subject rapidly without making contact, this intent was often thwarted by the somewhat erratic nature of the rat's movements under these conditions. As a result, some of the subjects came into infrequent contact with the model.

Behavior in the arena was transcribed from videotape (by observers not familiar with group assignments of individual subjects). Tapes were viewed multiple times to record subjects' location and locomotion, general behaviors not directed towards objects, (e.g., grooming), and investigation of the obstruction box. Day 1, in particular, was examined in some detail, to allow consideration of the possibility that the EC and IC rats reacted differently to the experience of being placed in this situation. Subjects' activity relative to the obstruction box was scored with respect to occurrences and durations for three behaviors that related to the obstruction box: leaning on the box (defined as placing one or both forepaws on the box and interrupting an imaginary plane, formed by extending the vertical walls upward, with the head); climbing onto the box (placing at least three paws in the top of the box); and entering the box (placing three paws inside the box). A summary measure (called a *box score*) was calculated as follows: leaning = 1, climbing = 2, and entering = 3. The day's box score was the value of the highest-scoring behavior exhibited, resulting in the subject receiving a score of 0-3 for each night. A total box score was determined by taking the sum of three nights' scores, including the 10 min sessions on Days 1 and 2 and the initial three minutes of Day 3 (prior to the emergence of the simulated predator).

RESULTS

Behavior in the arena on day 1 was examined in some detail, to allow consideration of the possibility that the EC and IC rats responded differently to the experience of being placed in the arena situation. This study would have been confounded if the behaviors of subjects in the arena had provided evidence that the EC and IC groups had been differentially stressed by the procedure. No such evidence was found. Behaviors relevant to predicting escape did, however, show EC-IC differences.

Group means and the results of statistical tests for several pre-challenge behavioral measures are reported in Table 1. On Day 1, no differences were found in locomotion (as measured by number of zone changes in the arena), or in time spent rearing or grooming. EC subjects spent significantly more time than IC investigating the obstruction box, and exhibited more involved interactions with the box (shown as "box score" in Table 1).

TABLE 1
Pre-Challenge Behaviors

| | IC | | EC | | | |
	mean	SEM	mean	SEM	F(1,14)	P
Day 1						
Zone changes	86.75	12.73	104.88	5.81	1.467	ns
Rearing (sec)	10.50	1.41	7.00	1.90	1.916	ns
Grooming (sec)	21.13	9.18	38.50	4.92	0.438	ns
Contact (sec)	19.00	7.00	87.75	18.40	10.669	< .01
Box score	0.75	0.15	2.13	0.21	24.200	< .001
Day 2						
Zone changes	95.87	12.43	76.88	7.07	1.545	ns
Box score	0.75	0.15	1.88	0.32	8.463	< .05
Contact (sec)	30.50	7.74	80.875	23.03	3.761	ns
Day 3 (3 min only)						
Zone changes	28.25	5.24	23.13	3.49	0.580	ns
Box score	1.13	0.328	1.75	0.385	1.336	ns

TABLE 1. Pre-challenge behaviors: Day 1 (10 minutes), Day 2 (10 minutes), and Day 3 (3 minutes prior to emergence of radio controlled model predator). Measures relative to the obstruction box were "Contact" (time in contact) and "Box score" (mean level of investigation of the box, as explained in the text).

There were no significant differences between the groups for locomotion and for time of contact with the box on Day 2 (see Table 1). Examination of types of interaction with the box on Day 2 again showed EC subjects as significantly more likely to climb and enter the box than IC subjects. On Day 3, pre-challenge locomotion (within the first 3 minutes of the session) did not differentiate between EC and IC subjects, and level of involvement with the obstruction box during this period was not significantly different between EC and IC groups.

A profile of behaviors under challenge (after the emergence of the simulated predator), adjusted to reflect proportion of pre-escape time rather than actual elapsed time to compensate for different amounts of time spent under challenge, is shown in Figure 1. Measures of these behaviors were quite variable; Analysis of Variance tests of most comparisons were nonsignificant. Relative amounts of time spent in investigation (sniffing at arena walls and floor and the simulated
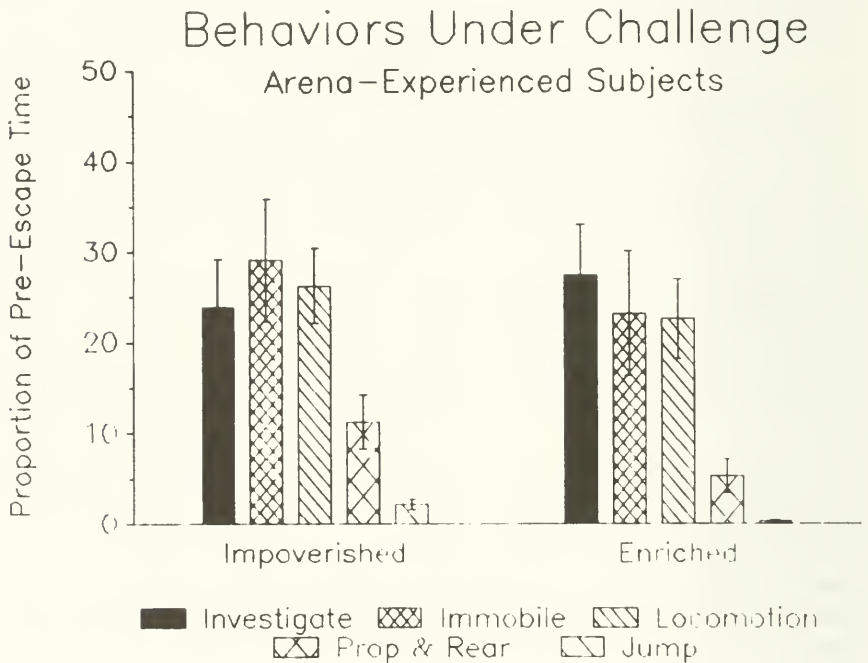
FIGURE 1. Behaviors under challenge, arena-experienced subjects. Bars are mean proportion of pre-escape time (or 180 second session) engaged in these behaviors; bars indicate SEM for each measure. IC subjects were more likely to jump ($p < .005$); all other comparisons were non-significant.

predator; $F(1, 14) = 0.238$), immobility ($F(1, 14) = 0.451$), locomotion ($F(1, 14) = 0.453$), and rearing or propping (leaning on arena wall; $F(1, 14) = 3.411$, $p = .083$) were all nonsignificant. IC subjects were significantly more likely than EC subjects to jump, usually in response to a near approach by the predator ($F(1, 14) = 12.023$, $p < .005$).

Time to escape under challenge was significantly lower in the EC rats. These times differed significantly from those for the IC rats ($F(1, 14) = 77.817$, $p < 0.001$); six IC rats failed to escape and were assigned

scores of 180 sec. The escape time distributions of EC and IC rats did not overlap. Behavior relative to the obstruction box during the three days was a good predictor of escape time under challenge (r = -0.795, $p <$ .001).

EXPERIMENT II

The results of experiment 1 demonstrate quite clearly that rats with experience in enriched and impoverished environments display a behavioral difference in response to apparent attack in an environment with which they have had opportunity to become familiar. The results cannot, however, rule out the possibility that the results of experiment 1 could be due to an environmentally induced difference in behavioral response to the stress of apparent attack rather than to intra-arena learning. In order to test this hypothesis, a second experiment was carried out eliminating the initial two days' experience in the arena.

METHOD

Animals

In Experiment 2, 12 naive male Sprague-Dawley rats were housed in standard colony conditions until the start of the experiment at 90 days of age.

Procedure

Procedures were identical to those used in Experiment 1, up until the point at which subjects were introduced into the arena. At this time, subjects were placed in the arena (configured as in Day 3 of Experiment 1) for three minutes, after which the motorized simulated predator emerged and began chasing the subject. Escape time was measured up to 180 seconds as in Experiment 1.


RESULTS

Behavioral profiles under challenge, again proportional to amount of time spent under challenge, are shown for IC and EC groups in Figure 2. For Experiment 2, all comparisons were non-significant, including relative amounts of time spent in investigation (F (1, 10) = 0.213), immobility (F (1, 10) = 1.497), locomotion (F (1, 14) = 0.403), and rearing or propping (F (1, 14) = 2.456), and jumping (F (1, 14) = 4.045, p = .07). As

in Experiment 1, EC rats escaped from the arena more quickly than IC (F (1, 10) = 9.426, p < .05); in fact, none of the IC subjects escaped within the 180 sec maximum time.

Trials were terminated at 180 seconds even though it was clear from pilot testing (in which rats that did not escape within 180 seconds did not escape at all, even given longer periods of being chased) that this would create a ceiling effect. Within 180 seconds the major questions of this study had been addressed; as a result, there was no further cause for continuing to stress the remaining rats. The only possible outcome that would embarrass the conclusion that inter-arena learning contributes significantly to later escape performance would be convergence of the groups with time in the arena; such convergence can be ruled out with these data in spite of the ceiling effect.

Combining the results of the two experiments yields a factorial experiment, with environmental condition and previous arena experience as between-subjects factors and escape time as the dependent measure. As shown in Figure 3, both the environmental condition and previous arena experience affected speed of escape. The effect of
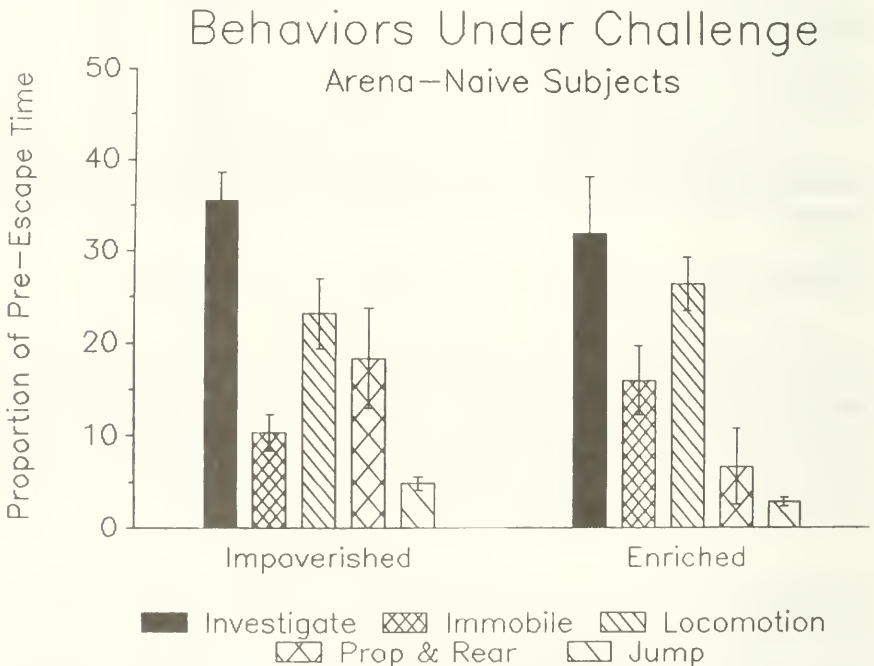
FIGURE 2. Behaviors under challenge, arena-naive subjects. Bars are mean proportion of pre-escape time (or 180 second session) engaged in these behaviors; bars indicate SEM for each measure. All comparisons were non-significant.

environmental condition was significant ($F(1, 24) = 64.46$, $p < .001$), as were the effects of previous experience in the arena ($F(1, 24) = 5.76$, $p < .05$) and the environment by experience interaction ($F(1, 24) = 4.67$, $p < .05$).
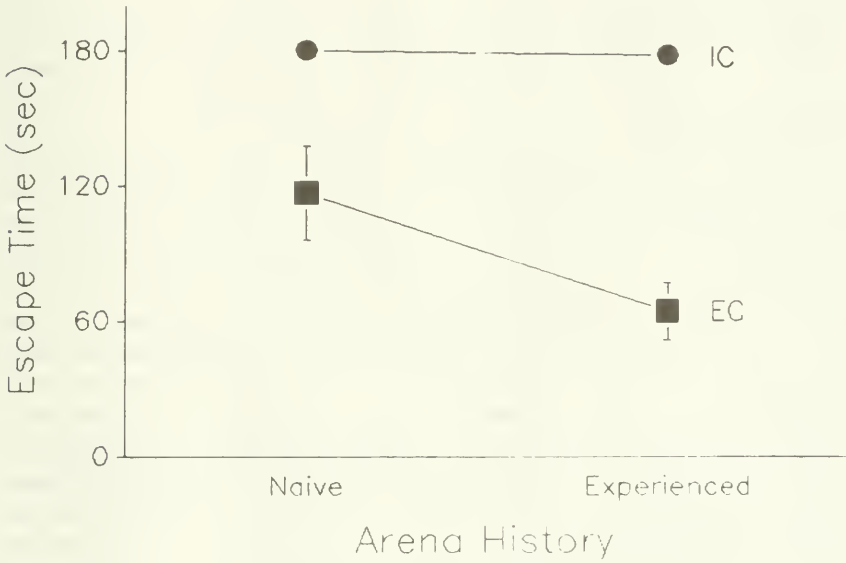
FIGURE 3. Summary figure: Effects of experience in arena and previous environmental treatment condition on escape time, to a maximum of 180 sec. Means for experienced animals are from data reported in the first experiment, naive animals from the second. Both main effects were significant, as was the condition-by-experience interaction. Standard error of the mean is shown for each EC group; standard error for each of the IC groups was smaller than the symbol used to plot the group mean.

DISCUSSION

The central question of this study was whether the particular behaviors employed in exploration influence the information gained as a result of that exploration. The behavior of the rats indicates that they do. These results demonstrate clearly that an animal can, by its own actions

or lack thereof, determine whether it gains information that may later have clear functional significance.

Although comparison of results from experiments run at different times opens the possibility of interference from extra-experimental variables, care was taken to minimize this risk: subjects for Experiments 1 and 2 were offspring from dams that were siblings, raised under identical colony conditions (approximately 40 days apart). Experi- mental procedures were identical other than for the experimental variable of pre-challenge arena experience. Limitations of equipment and of timing within the experiment prevented running this experiment initially as a two-factor design. In view of this, combination seems a valid tool for discussion.

There is a critical difference between these studies and the latent learning studies (Tolman & Honzik, 1930; Albert & Mah, 1972). In latent learning studies, the experimenters arranged situations in which sub- jects would, with very few exceptions, discover useful information; even random activity would lead to acquisition of this information. The behavior of the subjects themselves in those situations is of only minimal interest. In the experimental situation reported here, a random walk around the arena would not lead to discovery of the information that would later be useful. Instead, the subjects' behavior differed as a function of environmental history (a manipulation completed before subjects had access to the arena), and that behavioral difference determined whether the subjects gained information that was useful under later challenge.

The existence of an EC-IC difference in escape time on Day 1, when subjects have had little time to explore the arena, suggests that pre- existing differences in the behavioral hierarchies of subjects from IC and EC groups (previously documented in Renner and Rosenzweig, 1986, and Renner, 1987) do contribute to the results shown here. It is clear, however, that these pre-existing differences are not adequate as explanations of the EC-IC differences in escape time in Experiment 1 (arena-experienced subjects). In subjects given pre-challenge op- portunity to explore the arena, no differences were observed prior to challenge in behaviors indicative of stress.

The only behaviors in which differences were observed were those behaviors relevant to predicting escape. In addition, behaviors under challenge do not show evidence that EC and IC subjects were dif- ferentially stressed by the apparent attack. Two relatively brief and procedurally identical experiences in the arena did not diminish the differences in escape time, and may have amplified them (although the obvious ceiling effect imposed by the 180 second trial length limit makes it impossible to evaluate this conclusion statistically). Changes in behavior that occurred after the subjects' introduction to the arena must have been the result of events occurring in the arena, which must in

turn be the product of the behaviors of the subjects themselves; this implies the operation of positive feedback.

Had the simulated predator in this experiment been a genuine threat, those animal whose previous actions had led to discovery of an escape route would presumably have had a substantially enhanced chance of surviving the incident. Those animals whose behaviors had not led to this discovery would presumably have been more likely to be caught and would therefore have had a reduced chance of survival.

As reported previously (Renner, 1987) and reinforced here, movements in space and interaction with inanimate features of the environment are separable aspects of exploratory behavior. Although much is known of learning and memory for space and spatial relationships, or knowledge of investigation and manipulation of objects is considerably less complete. If the specific details of an animal's behavioral organization exert substantial influence on what that individual gains from an instance of exploration, then detailed study of the behavioral topography of exploration may provide information important for a full understanding of its role in animal information processing.

The evidence provided by these experiments is consistent with data from other studies: exploratory behavior can lead to acquisition of information. This may, in fact, be its function, to create situations for information gathering. In addition, these results indicate that the behaviors employed in exploratory behavior can determine the information acquired during exploration. Changes in the characteristics of an individual's exploratory behavior can therefore exert significant influence on that individual's ability to behave adaptively.

ACKNOWLEDGEMENTS

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