

BURYING AS A DEFENSIVE RESPONSE

IN RATS

by

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ABSTRACT

In typical laboratory settings, the defensive reactions of animals appear to be limited to freezing, fleeing, and attacking. However, in the present investigations, rats tested in the presence of movable material incorporated it into a striking and adaptive behavioural sequence. Rats shocked once through a stationary prod buried this shock source, even when the shock-test interval was 20 days. This burying behaviour occurred at a variety of shock intensities and seemed to be controlled specifically by the relation between the shock and the prod; rats shocked through a grid did not bury the prod, and rats shocked by one of two identical prods buried only the shock-prod. Both the position and brightness of the prod seemed to control the burying behaviour. When either of these cues was changed prior to the test, burying behaviour was disrupted compared to control conditions in which these cues were unaltered. Although burying was a directed and consistent response of rats to prod shock, it was not a simple, reflexive behaviour; rats could adapt their burying behaviour to changes in both the kind and disposition of burying materials. Thus, the usual assumption that the rat's defensive repertoire is limited to a few simple behaviours appears to have been shaped by the constraints of standard testing environments rather than by the actual propensities of the rat. These results were discussed in terms of their implications for a "biological" approach to aversive learning.

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INTRODUCTION

It has been argued that in order to understand animal avoidance learning, the subject's innate, defense reactions must be known (Bolles, 1970). This viewpoint has steadily gained credibility (e.g., Fantino, 1973; Mackintosh, 1974; Wong, 1976; Hineline, 1977; Schwartz, 1978), while the task of documenting the natural defensive behaviours of common laboratory animals has escaped serious attention. One reason the study of defensive responses has not progressed at a rate commensurate with its theoretical importance is the assumption that laboratory animals such as the rat are capable of only a few simple responses to environmental 'threats' (e.g., Bolles, 1975). However, studies that have shaped this view of the rat's natural defensive capacities have been conducted in laboratory settings that severely limit the subject's behaviour. The present studies provide evidence that apparent limitations in the rat's defensive ability are as much a function of the arbitrary experimental settings in which it has been tested as they are a product of biological constraints.

It is well established (e.g., Meyer, 1960) that only a few of an animal's behaviours can readily serve as avoidance responses. These data and the problem they pose for general theories of behaviour are briefly summarized in the first section of this Introduction. In the second section, Bolles' (1970) approach to this problem is presented. His view is that animals respond innately to dangerous events by fighting, fleeing, or freezing, and that it is only these defense reactions that can be readily learned in an avoidance task. However, in spite of the importance of Bolles' assumption that fighting, fleeing, and freezing are the only defense reactions available to experimental animals (Bolles, 1975),

he provides no empirical support for this view. Data supporting this assumption are reviewed in the third section of the Introduction. In the final section, this evidence is evaluated, and the rationale and purpose of the present investigations are presented.

Response problem

The purpose of much of the psychological research with animals conducted in this century has been to uncover the principles that underly the effects of experience on future behaviour. In experimental settings, 'behaviour' usually refers to a simple, quantified response such as salivation or bar-pressing; whereas, 'experience' typically refers to an arrangement of environmental events or stimuli that alters the likelihood of future responses. Stimuli that increase the probability of responses that they precede are frequently called conditioned stimuli, and stimuli that increase the probability of responses that they follow are called reinforcers. Out of these two basic arrangements of responses and stimuli have emerged the fundamental principles of classical and instrumental conditioning, respectively. It has often been assumed (e.g., Teitelbaum, 1966) that these principles apply uniformly to any species and to any combination of stimulus, response, and reinforcer (c.f., Shettleworth, 1972). This assumption has been called "equivalence of associability" (Seligman, 1970), and its validity has become the centre of recent debate.

There are many experimental findings that are consistent with the notion of "equivalence of associability". For example, Pavlov (1927) demonstrated that dogs could be trained to salivate in response to a wide variety of stimuli if these 'conditioned' stimuli had been followed by

food placed in the dog's mouth. Similarly, Skinner (1956) showed that various "schedules of reinforcement" resulted in comparable performance curves in a number of different species.

However, there is also evidence that seems to contradict the assumption of equivalence. In particular, there are many studies of avoidance learning that indicate that the principles that govern behaviour do not apply uniformly to all responses. Rats may learn to leap out of a chamber to avoid shock in one trial (Maatch, 1959), or learn to run down an alley to avoid shock in five trials (Theios, 1963), but take hundreds of trials to learn a lever-press avoidance task (Biederman, D'Amato, & Keller, 1964), if they learn it at all (D'Amato & Schiff, 1964). Similarly, pigeons can learn to avoid shock by shuttling to the 'safe' side of a box (Macphail, 1968) but have great difficulty avoiding shock by pecking a key (Hineline & Rachlin, 1969; Schwartz, 1973). It appears that orderly relationships between shock, stimulus, and response may be found in some situations but not in others (cf., Bolles, 1971).

Although these inconsistencies in the rates of avoidance learning suggest that the principles of behaviour change are not general, and that the response one chooses to condition with shock may be particularly important, alternative interpretations of the data have been offered (e.g., Berger & Brush, 1975). For example, the bar-press avoidance task is different from other avoidance tasks in a number of ways, any of which could account for differences in the rates of avoidance acquisition. Data that implicate these situational variables have come from studies primarily designed to facilitate bar-press performance in the rat. The acquisition of bar-press avoidance has been accelerated by:

- 1) reducing shock intensity (Bolles & Warren, 1965; D'Amato & Fazzaro, 1966)
- 2) administering brief, intermittent shocks instead of continuous shock (Brush, 1964; D'Amato, Keller, & DiCara, 1964; Hurwitz, 1964; Berger & Brush, 1975).
- 3) administering noncontingent shocks (Delprato & Holmes, 1977).
- 4) intensifying the signal (CS) for shock (Fantino, Sharp, & Cole, 1966).
- 5) lengthening the interval between shock (US) and its signal (Bolles, Warren & Ostrov, 1966; Berger & Brush, 1975).
- 6) increasing the distance between the CS and the manipulandum (Biederman, D'Amato, & Keller, 1964).
- 7) immobilizing the manipulandum during and shortly after shock (Forgione, 1970).
- 8) introducing the manipulandum at trial onset and retracting it after a response (Hull, Myer, & Smith, 1975).
- 9) shaping bar-press responses (Feldman & Bremner, 1963; Keehn & Webster, 1968).
- 10) prior appetitive conditioning (Galian & Schmalz, 1973).
- 11) handling animals between trials (Wahlsten, Cole, Sharp, & Fantino, 1968).
- 12) reducing the intertrial interval (Pearl & Fitzgerald, 1966).
- 13) reducing the size of the chamber so it is just large enough to accommodate the subject (Cahoon & Crosty, 1969; Azrin, Hopwood & Powell, 1967).
- 14) providing either exposure or access to a 'safe' compartment (Masterson, 1970; Crawford & Masterson, 1978).

- 15) interrupting the training schedule (Manning, Jackson, & McDonough, 1974).

It is clear from these data that a number of environmental variables can affect bar press avoidance performance; however, the question is whether the improvement attributed to these variables is of a magnitude sufficient to account for the overall variance in avoidance learning. In this context the most important conclusion that can be drawn from these data is that no environmental variables has been found that makes bar-pressing to avoid shock as easy for a rat to learn as jumping (Maatch, 1959) or running (Theios, 1963). Even in the most successful studies of bar-press avoidance (e.g., Hull, Myer, & Smith, 1975; Delprato & Holmes, 1977), it took about 200 trials before the major portion of subjects avoided shock consistently.¹ Although such results represent an improvement over earlier studies (e.g., D'Amato & Schiff, 1964), they cannot account for the vast differences in the rates at which different avoidance responses are learned.

By far the most powerful evidence against the "equivalence of associability" assumption was provided by a study of aversive conditioning by Garcia & Koelling (1966). These researchers found that rats associated a novel tasting solution with sickness, even after a long delay between the cue and the consequence; but they did not develop this "taste aversion" if the consequence was shock. Only if the solution was "bright and noisy" would rats avoid it if it had been followed by shock. These results clearly showed that each cue and each consequence could be quite effective, but only in certain non-arbitrary combinations. Because rats

¹"Stable" performance has been reported in fewer trials (Berger & Brush, 1975) but average avoidance was only 60%. It should also be noted that discrete trial procedures commonly used in training avoidance responses such as running or jumping are difficult to compare to 'free operant' procedures that are used in training bar-press avoidance.

seemed to associate only certain arrangements of cue and consequence these findings were clearly inconsistent with the equivalence of associability assumption.²

Traditional approaches to the study of behaviour have not been able to predict or explain these large differences in the ease of aversive learning. However, Bolles (1970) recently proposed a solution to this problem that was based on a general consideration of the survival requirements of the organism. It is Bolles' hypothesis that served as the focus for the present investigations.

The SSDR Hypothesis

Bolles argued that the survival requirements of an animal in its natural environment demanded a defensive mechanism other than avoidance learning as it is studied in psychology experiments. In the laboratory, a visual or auditory cue is often used to signal the onset of the aversive stimulus, but in the wild, predators do not often signal their prey before an attack. Furthermore, the researcher may wait many trials before stable avoidance performance occurs; whereas, a predator in the wild does not allow prey enough "trials" for "learning" to occur. Since most natural situations preclude this kind of trial and error learning, survival must instead depend upon a defensive mechanism with which the animal is already equipped, an innate set of defensive responses that occur in the presence of any new or sudden stimulus. Bolles called these responses 'species-specific' defense reactions (SSDRs) and assumed that they took one of only three forms: fleeing, freezing, or fighting.

Bolles utilized the notion of SSDRs to explain laboratory avoidance learning in the following way. The normally varied behavioural repertoire

² Recently, however, Krane and Wagner (1975) were able to demonstrate taste aversion learning when the 'consequence' was delayed shock.

of the domesticated laboratory animal is suddenly restricted when an aversive stimulus is presented. Now the animal, like its counterpart in the wild, emits only innate defensive responses; it either freezes, flees, or fights. Thus, aversive laboratory stimuli act in a manner similar to any sudden or novel stimulus in the animal's natural environment.

These defense responses emitted during shock bear the critical substrate upon which later performance in an avoidance situation depends. If the response required in the situation happens to coincide with one of the animals' SSDRs (e.g., fleeing), then training can proceed smoothly. If, on the other hand, the required response is not part of the animal's innate defensive repertoire, (e.g., bar-pressing) performance is uncertain and sometimes it does not progress beyond the base-line level. Thus, according to Bolles, an understanding of the variability in avoidance learning involves an appreciation of the organism's SSDRs and an assessment of the compatibility of these responses with the required avoidance response.

In Bolles' view, an avoidance response is acquired rapidly if it is an SSDR, not because it is strengthened (reinforced) by events that are contingent on this response (e.g., the avoidance of shock), but because competing SSDRs are suppressed (punished) by the aversive stimulus. For example, when the avoidance response is running down a straight alley, other SSDRs which compete with fleeing are quickly suppressed because they are paired with shock more often than is fleeing. Thus, the critical contingency for the rapid emergence of an SSDR is punishment (cf., Dinsmoor, 1954).

Bolles did agree that reinforcement could "strengthen" certain avoidance responses (Bolles, 1970; p. 42); however, he emphasized that

contingencies that are effective only after thousands of shocks (e.g., Herrnstein & Hineline, 1966) cannot possibly account for behaviour changes that take place in the laboratory after a few shocks, or, for that matter, how animals learn to survive in nature (Bolles, 1970). This emphasis on the ethological significance of avoidance behaviours is probably the most unique and compelling aspect of the SDDR hypothesis. Its apparent strength lies in its ability to predict laboratory avoidance behaviour from a knowledge of the organism's ~~idefensiveebehaviouraviour~~ defensive behaviour. Like any other hypothesis, however, its ultimate value depends on empirical tests of its validity.

The pivotal construct in Bolles' hypothesis is the notion of an innate defensive repertoire; yet Bolles paid little systematic attention to the defensive repertoire itself, except to specify that it is limited to freezing, fleeing, and fighting. What evidence, other than the fact that a particular avoidance response is learned rapidly, demonstrates that a behaviour is in fact an "innate," defensive reaction? ³ Bolles (1972) dealt with this problem in a footnote. The defensive repertoire of the subject can be determined by assessing its reaction to shock, and, "...anyone who does this with a rat will see that it either runs away, freezes, or becomes aggressive.." (Bolles, 1972, p. 129). Although Bolles did not conduct the study that he prescribed, there is now a growing body of literature that, for the most part, confirms his views. These data will now be reviewed.

Defensive behaviours of the rat

Freezing and fleeing. Blanchard and Blanchard (1969a; 1970a,b)

found that the predominant defensive reactions of rats exposed to stimuli associated with shock were freezing and fleeing. The rapidity with which

³It is also noteworthy that Bolles neglected to define the term, "innate defense reaction". For the purposes of the present investigation, a 'defense reaction' is viewed as an adaptive response to aversive stimulation. Nothing is assumed about the "innate" status, either than the suggestion (see

these responses developed suggested that they were 'unlearned', i.e., species-specific defense reactions (cf., Blanchard & Blanchard, 1971). Similarly, both of these responses were found to be prominent components of the rat's reaction to a cat (Blanchard & Blanchard, 1971; 1976). These responses occurred in the absence of prior experience with cats, and in the absence of agonistic contacts between the rat and the cat (cf., Curti, 1935). Blanchard, Kelley and Blanchard (1974) provided evidence that novelty itself can produce defensive reactions (cf., Bolles, 1970). They found that preexposure to a novel situation reduced rats' latencies to enter it. Conversely, rats fled from a novel to a less novel situation, even when required to cross an electrified grid. These results suggested that the hyperactivity observed in rats that are placed in novel situations may reflect abortive defensive reactions such as flight (cf. Walker, 1959). Many of the Blanchards' findings have been confirmed and extended in a recent study of the ontogeny of defensive reactions in the rat. Bronstein and Hirsch (1976) found that immobility in response to a footshock, a caged cat, or a suddenly moving object tended to increase as a function of the age of the rat. The similarity of the ontogeny of reactivity to the predator and to the footshock was interpreted as support for Bolles' (1970; 1972) contention that responses to stimuli associated with footshock represent innate defensive reactions (cf., Blanchard & Blanchard, 1971). This observation also appears to add some substance to Bolles' (1972) assertion that the attributes of the rats' natural defensive repertoire can be discovered by exposing the rat to 'unnatural' aversive stimuli such as shock.

Blanchard, Mast, and Blanchard (1975) designed an experiment to identify the particular features of cats that elicited freezing in rats. (general discussion) that there may be a strong genetic component to its expression.

They found that the sound and smell of a cat were relatively ineffective cues; whereas, visual cues associated with movement of the cat, whether it was alive or dead, were potent 'releasers' of freezing. Furthermore, the movement of a cat, a dog, or an inanimate card produced freezing, although the duration of the effect was less for the latter stimulus than for the other two. These experiments suggested that movement itself is an important 'releaser' of freezing in the rat, while the maintenance of freezing may depend on additional factors such as the phylogenetic 'relevance' of the releasing stimulus. Additional studies that control the size, speed, and shape of the releasing stimulus may clarify this issue.

Blanchard, Fukunaga, and Blanchard (1976) extended this line of research by examining other environmental factors that control defensive responding in the rat. They hypothesized that the type of defensive behaviour elicited in a rat by a cat (i.e., freezing or fleeing) might depend on the potential for escape from the test environment, and not necessarily on the differential punishment of defensive reactions as Bolles (1970) had suggested (but see Bolles, 1975a, 1976). In order to test this "elicitation" hypothesis, they employed their previous methodology (Blanchard & Blanchard, 1971) in which no defensive responses were followed by punishment (i.e., no rat-cat contact), with the additional provision that some rats were given a brief exposure to the inescapable test chamber prior to the introduction of the test stimulus. Rats that had been "familiarized" with the inescapable chamber were far less active when exposed to a cat than a similarly treated group that had not been familiarized. However, the activity scores of the more active group gradually declined over the 5-min test period until both experimental groups froze equally often but reliably more than a no-cat control group. Thus, freezing,

rather than flight, appears to occur when animals are "familiarized" with a situation in which escape is impossible. The Blanchards also argued that this factor seemed to account for the gradual activity reduction of the "non-familiarized" rats: their initial activity may have served to "familiarize" them with the inescapable environment and thus freezing gradually became their dominant defensive response.

Fighting. Fighting is another behaviour of rats that has been viewed as a defensive reaction (cf., Bolles, 1970; 1975; Blanchard & Blanchard, 1977). When a rat is placed in a chamber with another rat, or an inanimate object, and shock is administered, the rat will face the stimulus in an upright posture and attack it (for a review, see Ulrich, 1967). Ulrich and Azrin (1962) showed that this shock-elicited fighting can vary as a function of the duration, intensity, and frequency of shock; the size of the test chamber; and the initial orientation of the rats to each other. The age of the rats (Hutchinson, Ulrich & Azrin, 1965) and the duration of the shock test interval (Azrin, Hutchinson, & Sallery, 1964) can also affect shock-elicited fighting. It has been demonstrated in rats, hamsters, snakes, raccoons, opossums, monkeys, and cats (Ulrich et al., 1962; Azrin, 1964; Ulrich, Wolff, & Azrin, 1964). Even blinded rats can show shock-elicited fighting (Elory, Ulrich, & Wolff, 1965). Fighting can be elicited in the same manner by extreme heat (Ulrich, 1967), subcutaneous electrode shock (Ulrich et al., 1962), or physical blows (Azrin, Hake, & Hutchinson, 1964).

Blanchard and his associates (Blanchard, Blanchard, & Takahashi, 1977; Blanchard, Takahashi, & Kelley, 1977; Blanchard & Blanchard, 1977) have recently refined the analysis of defensive fighting. They studied agonistic interactions which occurred when rats from outside an established

laboratory colony were introduced to dominant male rats within the colony. Behaviours typical of the dominant males were piloerection, lateral display, and biting; whereas, the intruders boxed, froze, and lay on their backs, behaviours which appeared to inhibit aggression (Blanchard, Blanchard, Takahashi, & Kelley, 1977).

From these findings, the Blanchard's argued that the agonistic behaviours of colony rats and intruder rats appeared to fall into the categories of attack and defence, respectively. A similar examination of the agonistic behaviours of pairs of rats in a reflexive fighting task (see Ulrich & Azrin, 1962) revealed that the 'defensive' pattern (e.g., boxing) was far more characteristic of their behaviour than was the 'attack' pattern (e.g., biting). These observations suggested that the behaviours traditionally measured in the reflexive fighting task do not simply reflect "shock-elicited aggression" (cf., Ulrich & Azrin, 1962). Shock in the presence of a conspecific may instead elicit agonistic defense responses.

Pear, Moody, and Persinger (1972) conducted a study of shock-elicited fighting that was particularly relevant to Bolles' SSDR hypothesis. These researchers found that many lever-presses that ordinarily would be counted as instances of 'operant' avoidance were actually shock-elicited attacks at the lever. Thus, although Bolles' (1970) has suggested that rats 'learn' this task by being reinforced for inadvertently freezing on the lever, there are other 'species-typical' accounts of lever-press avoidance that are just as plausible.

Thigmotaxis. Grossen and Kelley (1972) studied an interesting defensive response that did not obviously fall into one of Bolles' three categories of defensive behaviour. They found that footshock increased thigmotaxis, i.e., the amount of time that rats spent in contact with the walls of the apparatus. In a second experiment, rats learned to jump from a grid to a

safe platform more readily when it was adjacent to the walls of the apparatus. These data supported Bolles (1970) argument that the acquisition of an avoidance response is enhanced if it is related to the organism's defensive repertoire. Although the evidence suggests that thigmotaxis should be added to the list of the rat's defensive behaviours, it is not clear that Grossen and Kelley's description of thigmotaxis represents anything more than a refined measure of freezing behaviour (i.e., freezing close to walls). In any case, these data should alert us to the possibility that knowledge of the rat's defensive capacities may be incomplete.

Rationale and Purpose

Rationale. The aforementioned studies of defensive behaviour confirm Bolles' view that freezing, fleeing, and fighting are defensive behaviours. However, since there does not appear to have been any concerted effort to identify defensive responses other than freezing, fleeing, and fighting, Bolles' assumption (Bolles, 1975) that all defensive behaviours fall into one of these three categories remains untested. Because Bolles argues that avoidance learning involves the elimination by punishment of all defensive responses in an animal's repertoire until only the most effective one remains, accurate predictions about avoidance learning must be based on a knowledge of an animal's complete defensive repertoire.

It is apparent from the literature on defensive reactions (e.g., Ulrich & Azrin, 1962; Blanchard & Blanchard, 1976) that a particular defensive behaviour may depend upon certain environmental 'supports' for its full expression. For example, an avenue of escape may support fleeing behaviour; the absence of support for fleeing and fighting may lead to freezing. To some researchers (e.g., Bolles, 1972), these observations simply

suggested that a particular test situation may favor one of the three defensive reactions. However, taken one step further, these observations suggest that the probability of discovering the full extent of the rat's defensive repertoire may vary as a function of the variety of situations in which defensive behaviours have been studied. Appropriate environmental conditions may be necessary for certain defensive behaviours to occur. Simply shocking a rat on a grid floor is, therefore, an insufficient test of the proposition that the "frightened" rat can only freeze, flee, or fight (cf., Bolles, 1972; 1975).

Traditionally, behavioural scientists have restricted the behaviour of their subjects to one or two alternatives in order to study the processes that presumably underlie all behaviours (e.g., Pavlov, 1927). Although this experimental tactic may have revealed some principles of classical and instrumental learning, its application seems inappropriate when the object of study is the discovery of behaviours. In order to discover behaviour, the makeup of the experimental setting should be tailored less for the restriction of behaviours than for their proliferation. Most of the research on defensive behaviours has been restrictive. The research has been inappropriately controlled in the sense that it has been confined mostly to situations similar to those in which avoidance phenomena have been traditionally studied (e.g., Blanchard et al., 1969, 1970). It is not surprising, therefore, that the defensive behaviours observed in these situations should be quite consistent with what "anyone"⁴ can see

⁴Bolles (1972, p. 129)

in standard avoidance apparatuses, and not at variance with what are assumed by psychologists to be the rat's characteristic modes of defense. In short, I am suggesting that the expression of the rats' defensive capacities has been shaped more by the constraints of typical laboratory test environments than by the rat itself.

Purpose. The study of the rats' defensive repertoire may be facilitated by altering the standard laboratory setting so that arbitrary constraints on the rat's behaviour are reduced. Although a variety of test environments have been widely used to investigate the responses of laboratory animals to aversive stimulation, most have one feature in common: the floor of the apparatus is a rigid metal grid through which feces and urine can drop and shock can be administered. This feature may constrain defensive behaviour in two ways. First, unlike more natural settings, there is little if anything on the floor of the apparatus that the rat could move or manipulate for its own defense. Second, the aversive stimulus in this setting is relatively diffuse and may not support a defensive behaviour that is normally directed at localized sources of aversive stimulation.

Preliminary work in this laboratory has supported this hypothesis. We found that a rat housed in a chamber with bedding material (San-i-cel) often pushed this material toward and over (i.e., buried) a well-defined shock source. This burying behaviour could be a fundamental part of the rat's defensive repertoire, and thus a more systematic study of this response was warranted.

The general purpose of the present investigations was to contribute to the development of a viable 'biological' approach to avoidance learning by studying the burying response. The purpose of each study was

to provide two kinds of evidence to support the view that burying behaviour is a prominent defensive response of rats. Each experiment was designed to show that burying is a reliable response to localized aversive stimulation, and/or to show that the burying response is adaptive; that is, that it affords the animal some protection from the noxious agent.

GENERAL METHODS

This section contains a description of the methodological features common to each of the nine experiments in this thesis. In each experiment, the effect of forepaw shock on the amount and duration of burying behaviour in rats was assessed.

Subjects. The subjects in each of the experiments were 250- to 550 g male, hooded rats purchased from Canadian Breeding Farm and Laboratories, La Prairie, Quebec. Each rat was individually housed in a 24 x 18 x 18 cm wire-mesh cage under controlled illumination (12-hr light/dark cycle) with continuous access to Purina laboratory chow and water.

Apparatus. Animals were tested in a small, closed room, adjacent to the behavioural recording apparatus. Behaviours were viewed via closed circuit television and recorded on video tape.

Inside the testing room, a television camera was mounted 50 cm directly above the 44 x 30 x 44 cm transparent Plexiglas test chamber. The chamber floor was covered evenly for the duration of each experiment with 5 cm of regular grade Saniclelf, a commercial bedding material made of ground corn cob. (Paxton Processing Co., Paxton, Illinois). In the center of each of the four walls of the chamber, 2 cm above the level of the bedding material, was a hole 1.2 cm in diameter through which a wooden prod (6.5 x 0.5 x 0.5 cm) could be inserted. In some experiments, two prods were inserted through the holes at opposite ends of the chamber. Shocks were delivered through the two uninsulated wires wrapped around the stationary prods.

Procedures

Habituation: Prior to each experiment, all animals were handled and placed in the Plexiglas test chamber in groups of five or six for

30-min periods on each of 4 consecutive days.

Shock administration. On the 5th day, the shock prod was introduced into the experimental chamber through the hole in an end wall; then, each experimental animal was placed individually in the centre of the chamber facing away from the prod. When each experimental subject first touched the prod with a forepaw, a brief shock, initiated by the experimenter and terminated by the withdrawal of the subject, was delivered from an 800 V AC power source. The single shock elicited a sudden withdrawal toward the back of the chamber that in most cases was accompanied by vocalization. In some experiments the rats were removed from the chamber immediately after shock and returned later for testing; however, in most cases, the shock signalled the beginning of the test session.

Current from the 800 V power source was attenuated with a series dropping resistor. In all but one experiment, the value of the dropping resistor was 80,000 ohms. The current flow in this shock circuit was monitored by a storage oscilloscope to determine the actual intensity and duration of shocks received by rats under the conditions in which they would be tested. The 10 naive, adult, hooded rats selected for this purpose received shocks that averaged 7.9 mA in intensity ($SD = 1.47$), 42.9 msec. ($SD = 9.8$) in duration.

Behavioural observation and quantification. The behaviour of each subject was viewed for the 15 min test period, and the incidence and duration of burying sequences were recorded on an event recorder.

The burying behaviour of rats in this situation consisted of a series of stereotyped sequences that began with the rat facing the prod from a distant part of the apparatus. The rat then moved directly toward the prod, pushing and spraying a pile of bedding material over the prod with

its snout and rapid movements of its forepaws. Often, this behaviour was punctuated by periods when the rat stretched forward, its vibrissae nearly touching the prod before withdrawing abruptly to the rear of the chamber from where it began another sequence of pushing and spraying. The invariant component of this behavioural pattern was the rapid, alternating, forward-motion of the forelimbs by which the rat displaced material toward the prod. It was the durations of these directed bursts of forelimb spraying that were monitored by the experimenter, and that defined burying behaviour in the present thesis. Routine checks of videotaped test sessions always corroborated the original measures,

After each test, the height of the bedding material from the floor of the Plexiglas chamber was measured at the junction between the prod and the wall. This measure, and the ratio formed by the height of the highest mound over its distance from the prod, served as additional indices of burying behaviour.

Statistical analysis. In most cases, the designs of the experiments presented in this thesis justified a priori statistical analyses. An a priori comparison of central interest in the early experiments was between the mean scores of shocked and unshocked rats; in subsequent experiments the comparison was between the mean scores associated with 'shock' and 'control' prods. In general, the overall effect of the shock was so clear that casual inspection of individual scores was as convincing as the results of statistical analyses. Analysis of variance was occasionally used to evaluate effects that could not be assessed by individual comparisons.

Experiment 1

The purpose of Experiment 1 was to demonstrate that when adequate materials are available burying is both a prominent and enduring response of rats to aversive stimulation.

Method

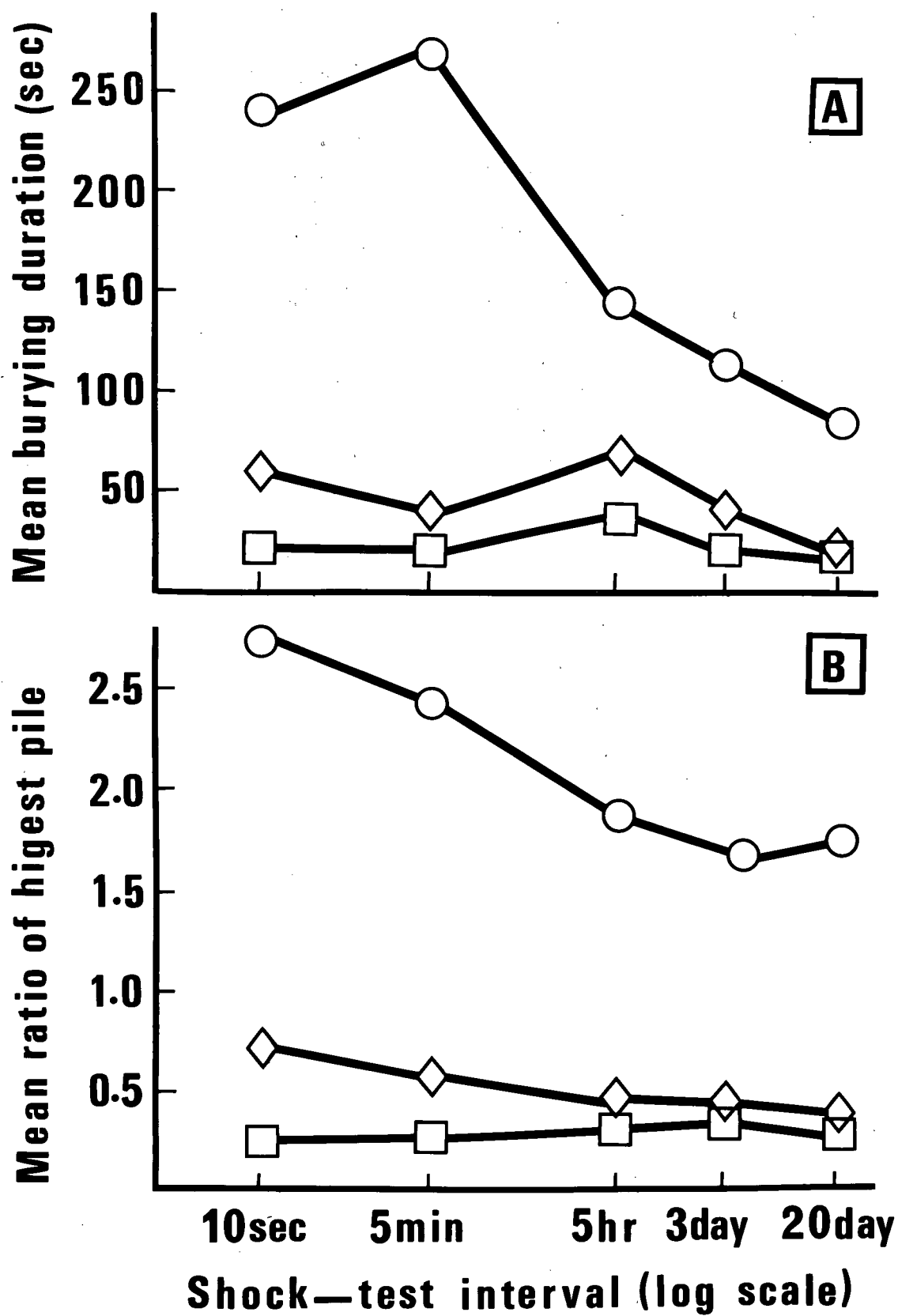
After 4 days of habituation, the 120 rats were randomly assigned to one of three basic conditions on Day 5. The rats in one condition (shock subjects, $n = 60$) were shocked (8 mA) from a single prod in the manner previously described. Following the shock, each of these subjects was removed from the chamber. Rats in the second condition (prod controls; $n = 30$) were not shocked but otherwise were treated in the same manner. Subjects in the third condition (no-prod controls, $n = 30$) were placed individually in the test chamber for a few seconds but were exposed to neither the shock nor the prod.

The rats in each of the three conditions were returned to the chamber for a 15-min shock-free test with the prod 10 sec, 5 min, 5 hr, 3 days, or 20 days later. Thus, 12 shock rats, 6 prod control rats, and 6 no-prod control rats were tested at each of the five intervals. The behaviour of each animal was viewed and recorded by closed circuit television as described in the General Methods section.

Results and Discussion

Figure 1 shows that burying was a prominent part of the behavioural repertoire of the shocked subjects. Two-way analysis of variance of the "duration" data (Figure 1, Panel A) restricted to the two control conditions revealed no significant effects ($p > .05$). However, planned orthogonal

Figure 1. Mean duration of burying (Panel A) and the mean of the ratio between the height of the highest pile and its distance from the prod position (Panel B) at each of the shock-test intervals for subjects in the shock (circles), prod control (diamonds), and no-prod control (squares) groups.



comparisons between the duration of burying in the shocked and the control subjects combined at each of the five shock-test intervals indicated that shock subjects spent significantly more time burying at each interval (10 sec, $t(22) = 4.01$, $p < .0005$; 5 min, $t(22) = 5.93$, $p < .0001$; 5 hr, $t(22) = 2.48$, $p < .05$; 3 days, $t(22) = 2.19$, $p < .05$; 20 days, $t(22) = 2.61$, $p < .02$).

The present data clearly demonstrate that in the presence of adequate materials burying is a prevalent response of rats to aversive stimulation. At the two shortest shock-test intervals, rats engaged in burying for about 25% of the entire test period, and the duration of burying at intervals as long as 20 days was still well above control levels. At no time were rats observed to push or spray material in any direction other than toward the prod.

The height of the highest pile accumulated by each rat divided by the distance of the peak of that pile from the usual prod position formed a ratio which served as the basis for objectively assessing the relative effectiveness of each rats' burying behaviour. Rats with large height/distance-from-prod ratios were those that accumulated the highest piles closest to the prod position. It is clear from Figure 1 (Panel B) that these ratios provided an independent and objective confirmation of the behavioural data. Although there were no significant differences between the two control conditions ($p > .05$), planned orthogonal comparisons between the shock and combined control means at each of the shock-test intervals revealed significant differences (10 sec, $t(22) = 3.42$, $p < .005$; 5 min, $t(22) = 3.23$, $p < .005$; 5 hr, $t(22) = 2.32$, $p < .05$; 3 days, $t(22) = 2.09$, $p < .05$; 20 days, $t(22) = 2.89$, $p < .01$).

Experiment 2

The purpose of Experiment 2 was to determine whether rats shocked in one environment would bury the source of an aversive stimulation when confronted with it in another.

Method

The 20 naive rats, handled and exposed to the test chamber on the first 4 days, were randomly assigned to shock ($n = 10$) or control ($n = 10$) conditions on Day 5. Each experimental rat was shocked when it contacted a prod inserted through the wire mesh of its home cage. Then the prod was removed and mounted on the wall of the test chamber. The controls received the same treatment but were not shocked. All subjects were tested in the chamber 1 min following prod contact.

Results & Discussion

When rats were confronted in the test chamber with a prod through which they had been shocked in their home cages, they buried it. The shocked animals ($M = 108$ sec) spent significantly ($t(18) = 3.16, p < .005$) more time burying the prod than did the control ($M = 5$ sec) rats. Furthermore the height/distance-from-prod ratios were far greater ($t(18) = 4.29, p < .0005$) for the piles of bedding material accumulated by the shocked animals ($M = 6.2$) than for those accumulated by control ($M = 0.7$) subjects.

Experiment 3

In Experiments 1 and 2, rats buried the prod through which they had been shocked. Would the rats have buried this test object if they had received shock from a different source? In other words, is shock per se

a sufficient condition for burying, or must the shock be administered through the test object?

Method

The methods were the same as those of Experiment 2 except that on Day 5 the shock animals ($n = 15$) were shocked (1 sec, 2.5 mA)⁵ through the floor of a 43 x 21 x 29 cm grid box 1 min before being exposed to the prod on the wall of the test chamber. The control animals ($n = 10$) were not shocked but were otherwise treated in the same way.

Results and Discussion

The results of Experiment 3 indicated that shock per se is not a sufficient condition for the burying response. Neither the grid-shocked animals ($M = 6$ sec) nor their unshocked controls ($M = 2$ sec) spent substantial periods of time burying the prod. This observation was confirmed by an examination of the height/distance-from-prod ratios for the highest piles of bedding material accumulated by the shock ($\bar{X} = 0.8$) and control ($\bar{X} = 0.3$) subjects. Thus, the two groups did not differ significantly in terms of either measure (duration of burying: $t(23) = .61$, $p > .50$; height/distance-from-prod ratio: $t(23) = .55$, $p > .50$).

The behaviour of the grid-shocked animals in Experiment 3 was, thus, in striking contrast to the performance of the prod-shocked rats in Experiment 2. The latter subjects spent an average of 108 sec accumulating piles of bedding material with height/distance-from-prod ratios averaging 6.2.

Although the contrasting results of Experiment 2 and Experiment 3

⁵

Although there is no obvious way to equate the intensity of shock that rats receive through a grid floor with the intensity they receive through the prod, the initial behavioural reactions of rats to grid-shock at these parameters seemed to be comparable to their initial reaction to prod-shock at the parameters used in previous experiments.

Experiment 4

The purpose of Experiment 4 was to show that rats bury sources of shock despite substantial variations in shock intensity.

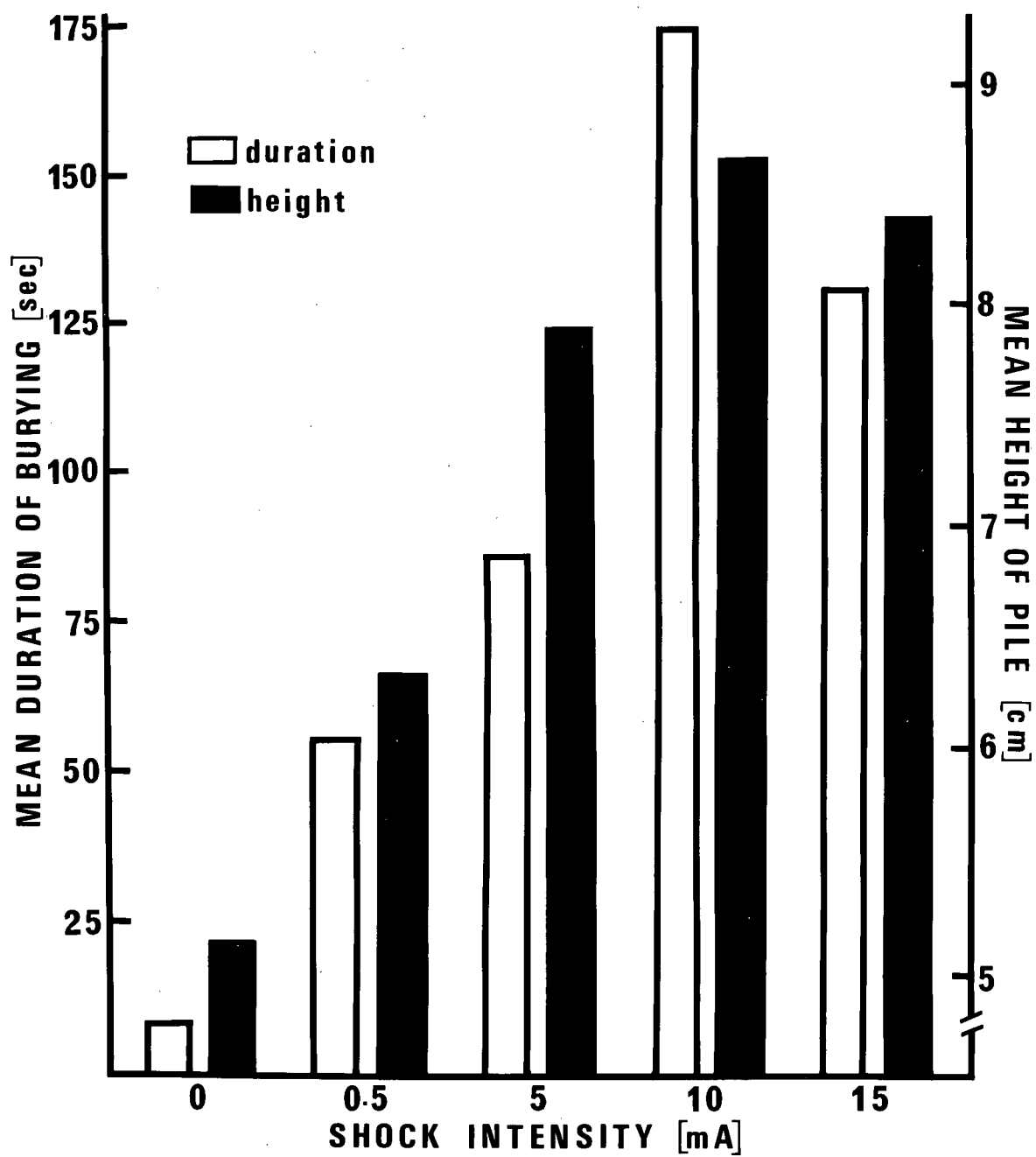
Method

On Day 5, the 60 naive rats were randomly assigned to one of five conditions ($n = 12$). Every animal was treated in the same manner throughout the experiment, except that the intensity of the shock was varied for subjects in each condition. Upon first contacting the prod, the experimental rats were shocked at .5, 5.0, 10.0, or 15.0 mA, whereas the control rats were not shocked. Shock intensities were manipulated by adding the appropriate resistor in series with the 800-V shock generator. The actual current flow was oscillographically recorded in each case. Following prod contact, each subject was removed from the test chamber for 1 min before being returned to the chamber for the 15-min observation period.

Results and Discussion

Figure 2 shows that rats buried the localized source of shock at a variety of shock intensities. A priori comparisons between each experimental group mean and the control group mean confirmed that shock subjects spent significantly more time burying the prod at each shock intensity except .5 mA (duration of burying, .5 mA, $t(22) = 1.36$, $p < .10$; 5 mA, $t(22) = 3.91$, $p < .0007$; 10 mA, $t(22) = 4.23$, $p < .0003$; 15 mA, $t(22) = 5.29$, $p < .00002$). A similar analysis of the "height" data corroborated the behavioural results.

Figure 2. Mean duration of burying and the mean height of bedding material at the prod for each of five shock intensities.



(Height at prod, .5 mA, $t(22) = 1.18$, $p > .10$; 5 mA, $t(22) = 2.96$, $p < .01$; 10 mA, $t(22) = 3.14$, $p < .004$; 15 mA, $t(22) = 3.50$, $p < .002$).⁶

Evidence of a positive relationship between shock intensity and the amount of burying was provided by a product moment correlation coefficient computed between each experimental animal's oscilloscopically-determined shock intensity and its duration of burying score. The resulting coefficient of .285, although it did not account for a large part of the variance, was significant at $p < .05$.

Taken together, these results confirm that burying occurs reliably at a variety of shock levels, and thus it is difficult to attribute the extreme differences in the results of Experiment 2 and Experiment 3 to divergent shock parameters. Although burying seems to be facilitated as shock intensity is increased (cf., Ulrich & Azrin, 1962), vigorous burying behaviour occurred at all shock intensities. Thus, variations in shock parameters may not have as great an effect on burying behaviour as variations in the relationship between the shock and the test object; rats shocked through the test object buried it (Experiment 1 and 2), whereas rats shocked from a different source did not bury the test object (Experiment 3).

Experiment 5

To argue convincingly that a particular behaviour is a defensive response, two basic conditions must be met. First, the behaviour must be shown to occur in response to aversive stimulation. In this regard, bury-

⁶Because the a priori comparisons in this study were nonorthogonal (Winer, 1962), a per-comparison alpha level of .0125 was utilized, making the overall experiment-wise alpha .05.

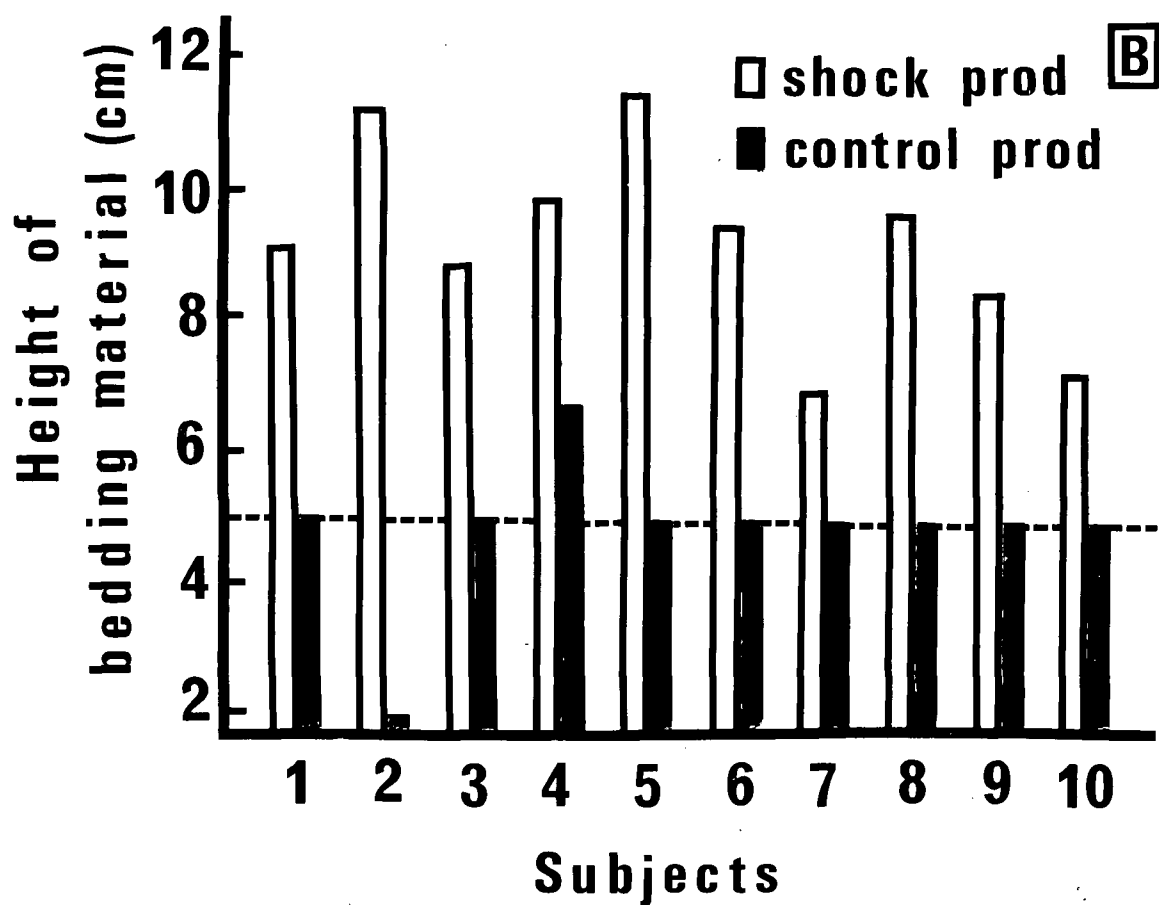
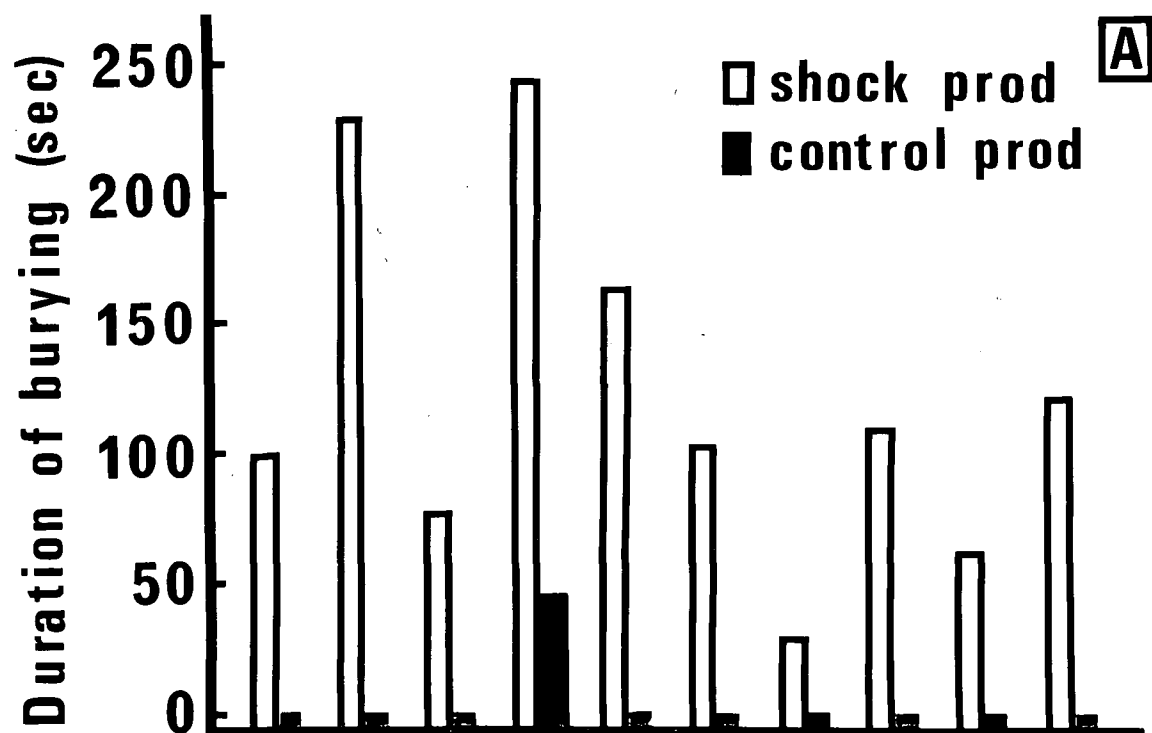
ing was found in Experiments 1, 2, and 4 to be a common response of laboratory rats to prod shock when the appropriate materials were available. Second, the response must be adaptive; that is, it potentially must afford the animal some protection from the noxious agent. In order for burying to be adaptive it must be directed, but more importantly, it must be directed at the source of aversive stimulation. It is difficult to see how burying directed at neutral objects following aversive stimulation could be adaptive. While the burying behaviour of the shocked rats in Experiment 1, 2, and 4 clearly was directed at the prod, it was not clear whether the burying behaviour was directed at the prod because of its previous association with shock; burying may have been directed at the prod because it was the only object in the test chamber.

When considered together, the results of the first four experiments do provide some support for the view that the prod was buried because of its previous pairing with shock. The rats shocked by the prod (Experiments 1, 2 and 4) buried it; whereas, those that received grid shock (Experiment 3) did not. However, like the results of all "negative" experiments, the results of Experiment 3 must be interpreted with caution. The purpose of Experiment 5 was to provide more conclusive evidence relevant to this issue.

Method

On Day 5, two identical prods were mounted on the walls of the test chamber, one at each end. The behaviour of each of the 10 naive subjects was recorded for 15 min after it had been shocked (8 mA) by one (randomly predetermined) of the two prods. Before shock, each animal was allowed to contact each prod at least once without being shocked.

Figure 3. Duration of burying (Panel A) directed at the shock prod and control prod and the final height of the bedding material at the shock prod and control prod (Panel B) for each of the subjects in Experiment 5. (At the beginning of each session the height of the bedding material was 5 cm in all parts of the test chamber).



Results and Discussion

The results of Experiment 5 were so clear that inspection of individual scores (Figure 3) rendered statistical analysis of group scores superfluous. All 10 subjects spent time burying the prod through which they had been shocked ($M = 125$ sec); whereas, only one subject briefly attempted to bury the control prod, but not until the shock prod had been completely covered. Similarly, all 10 subjects accumulated higher piles of bedding material at the shock prod than at the control prod. One subject (Subject 2, Figure 3) actually removed material from under the control prod to bury the shock prod.

Experiment 6

The results of Experiment 5 provided further evidence that the burying behaviour was being controlled specifically by the relation between the prod and the shock; rats selectively buried the prod that was paired with shock. Thus, burying appears to be a potentially adaptive response of rats to specific environmental 'threats'. However, although it is clear that burying was directed toward the aversive stimulus, the results of previous experiments did not indicate which of the many cues in the experimental setting actually controlled the response. Traditional methods of studying the stimulus control of behaviour (Skinner, 1938; Tinbergen, 1951) were employed to approach this issue in the next two experiments. The specific purpose of both Experiments 6 and 7 was to determine whether burying behaviour changes systematically when the position and/or brightness of the prod are changed after prod-shock.

Method

On the fifth day each of the 50 naive rats was randomly assigned to one of five groups of 10 subjects (four experimental groups and one control group), before being placed individually in the centre of the chamber facing away from the prod. The end of the chamber to which the prod had been fixed (front or back) and the brightness of the prod (black or white) were randomly pre-determined for each rat before the test began. As each experimental animal touched the prod, the 8 mA shock was administered in the usual way; immediately following shock the subject was removed. Control subjects ($n = 10$) were treated in exactly the same manner except that shock was not administered.

Each rat in the four experimental groups ($n = 10$) was individually placed in the chamber 1 min later with either, 1) the same prod (black or white) on the same wall, 2) the same prod on the opposite wall, 3) the different prod on the same wall, or 4) the different prod on the opposite wall. Either two or three control rats were tested with each of these four stimulus combinations.

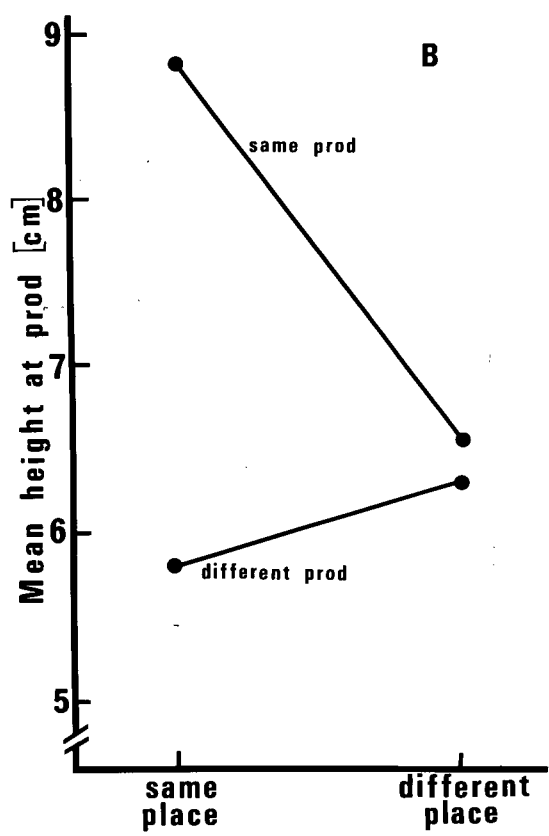
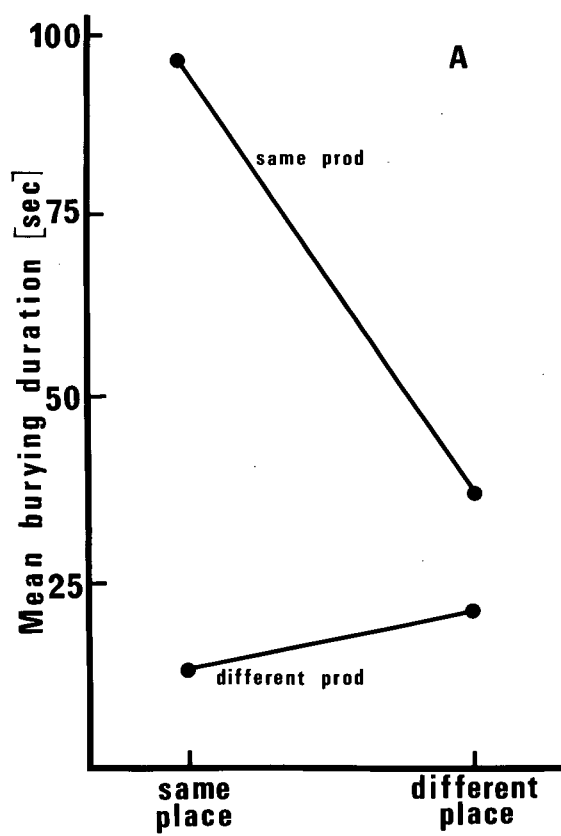
Results and Discussion

Almost all of the rats in the four shock groups moved some material toward the prod. All 10 animals tested with prod brightness and position unchanged engaged in some burying, while burying behaviour was observed in 10, eight, and eight of the subjects in the "same prod-different place," "different prod-same place," and "different prod-different place" groups, respectively. On the other hand, burying behaviour was almost nonexistent in unshocked, control subjects. Only three of the 10 control rats directed bedding material at the prod, and none of these did so for more than 5 sec.

Thus, the mean duration of burying behaviour was less than a sec for control subjects, and the mean height of bedding material accumulated at the prod was less than 0.1 cm greater than the initial level of 5 cm. An a priori comparison between the combined experimental group means and the control mean confirmed that the duration of burying by shocked rats was significantly greater than that of control rats $F(1,45) = 11.34, p < .002$. Similarly, the height of material accumulated at the prod by shocked rats was significantly greater than that accumulated by control rats $F(1,45) = 9.18, p < .004$.

Control of the burying behaviour of the experimental subjects by brightness and position cues is illustrated in Figure 4. Changing either the brightness of the prod and/or its position decreased both the duration of burying (Panel A) and the height of material accumulated at the prod (Panel B) relative to the performance of experimental subjects tested with prod and position cues unaltered. The data were subjected to a two-way analysis of variance, the two factors being brightness and position, each with two levels (same or different). The analysis of the "duration" data revealed a significant interaction between brightness and position $F(1,36) = 7.11, p < .01$. Multiple comparison tests (Dunn's Test, critical difference = 46.89, $p < .05$) indicated that changing either brightness or place cues led to a significant reduction in the duration of burying but that changing both cues together did not produce a significantly greater reduction. A comparable set of analyses of the "height" data confirmed these behavioural results. The interaction effect was again significant $F(1,36) = 5.53, p < .02$; the subjects tested with neither brightness nor position cues changed accumulated significantly higher piles at the prod than did the rats in the other three experimental groups, and these latter three

Figure 4. Mean duration of burying (Panel A) and the mean height of bedding material at the test prod (Panel B) for each of the four cue combinations.



groups did not differ significantly from each other (Dunn's Test, critical difference = 2.17, $p=0.05$).

Although in the first five experiments, rats had never been observed to push bedding material in any direction other than at the shock source, 8 of the 40 shocked animals in the present experiment directed bedding material at the hole in the wall of the apparatus directly opposite the prod position. However, such responses were restricted to subjects in the two conditions in which the position of the prod had been changed ($\chi^2(1) = 10$, $p<.005$). After burying the prod in its new position, these subjects sprayed bedding material at the hole through which the prod had been inserted during shock administration. No animal ever directed bedding material at the holes in the centre of the two side walls.

The results of Experiment 6 demonstrated that both the brightness and position of the prod exerted some control over the burying response after only a single prod-shock pairing. When the position of the prod was unchanged, changing the brightness of the prod (from black to white or from white to black) significantly reduced the amount of burying. Similarly, if the brightness of the prod was held constant, moving it to the opposite wall during the test substantially reduced prod burying. The identity of the cues that defined the location of the prod was not readily apparent since external room cues were visible through the Plexiglas walls of the test chamber in addition to tactual, olfactory, and visual cues provided by the chamber itself.

Control of the burying behaviour by brightness and position cues was not additive (Weiss, 1972); changing both cues did not significantly reduce the level of burying below that observed in the two conditions in which only one of the cues had been changed.

The fact that some of the rats in the two groups in which the position of the prod was changed buried the hole on the other end of the chamber through which the prod had been inserted during shock administration suggests that position cues were important in more than one sense. Not only did position cues exert control over burying by their role in defining prod position but location cues that were associated with the shock were themselves capable of inducing the burying response in some subjects.

Experiment 7

In Experiment 7, stimulus control of burying was investigated using a simultaneous discrimination procedure (Experiment 5); each subject was shocked and tested in the presence of two prods.

Method

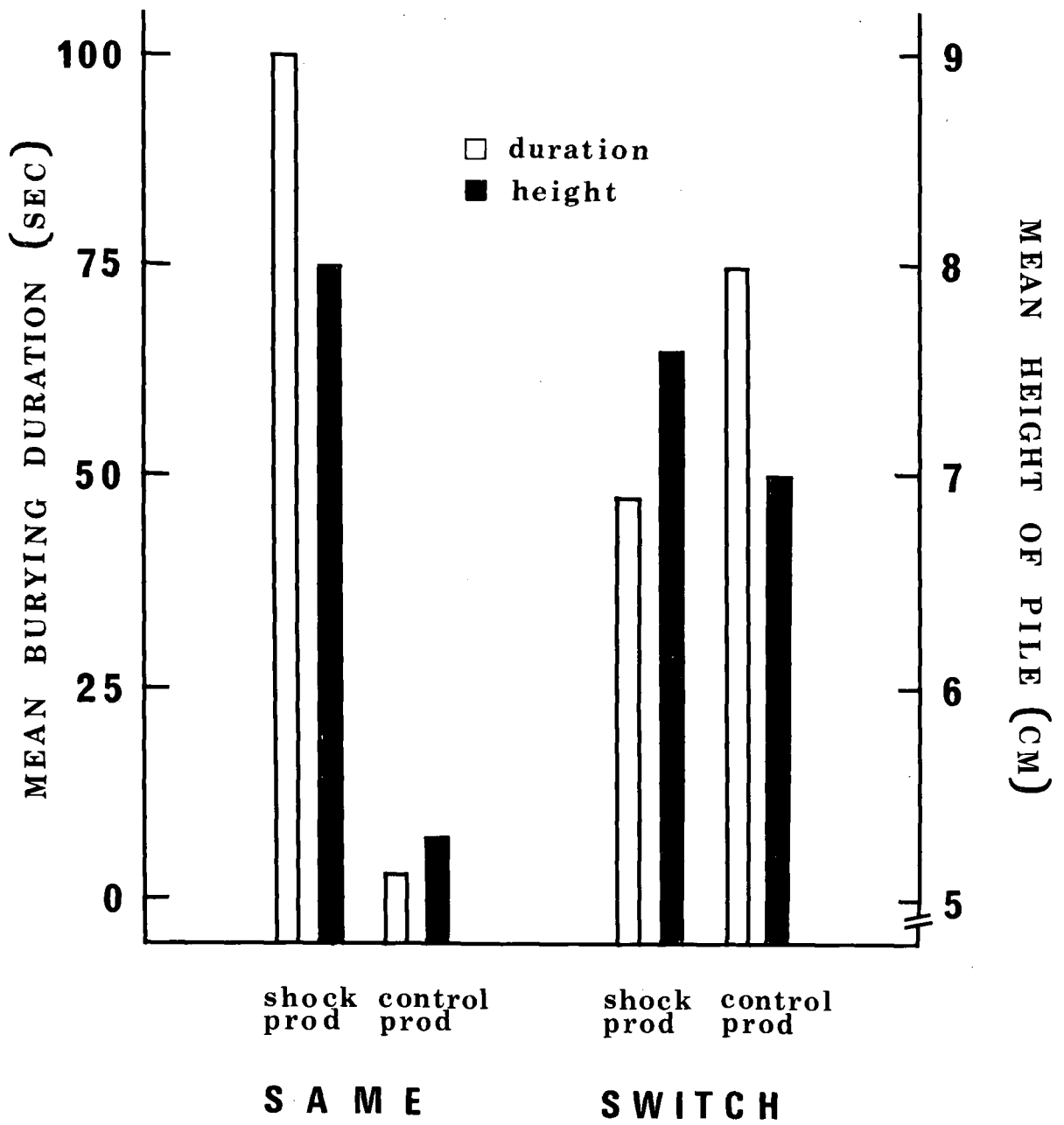
The 24 naive hooded rats were randomly assigned to Switch ($n = 12$) or Same ($n = 12$) conditions. On Day 5, all subjects were shocked once when they contacted either the black prod or the white prod which had been mounted through the holes at opposite ends of the test chamber. It was randomly predetermined which subjects would be shocked by which prod, with the proviso that half the subjects in each of the two groups were shocked by each prod. Before shock, each subject was allowed to contact each prod at least once. Immediately after shock, each subject was removed from the test apparatus for 1 min. Each subject in the Same Condition was then returned to the chamber with the prods in their original positions; whereas, subjects in the Switch Condition were returned to the chamber with the positions of the prods reversed.

Results and Discussion

Although the incidence of burying was comparable in the two conditions (10 of the 12 subjects in each condition displayed some burying), there was a striking difference between the two conditions in the direction of the burying. It is apparent from Figure 5 that those rats tested with the prods in their original positions directed almost all of their burying activity at the prod through which they had been shocked; whereas, when the positions of the prods were reversed prior to the test, the burying behaviour was distributed almost equally between both prods.

The significance of the differences represented in Figure 5 were evaluated with a series of t -tests for dependent measures. In the Same Condition, subjects spent significantly more time burying the shock prod than they did burying the control prod [$t(11) = 4.60$, $p .0008$] and the height of the bedding material accumulated by these animals at the shock prod was significantly greater than the height accumulated at the control prod [$t(11) = 4.81$, $p < .0005$]. These results are essentially the same as those obtained in Experiment 5, where basically the same procedure was used. In contrast, in the Switch Condition an analysis of both the height [$t(11) = 1.27$, $p > .1$] and duration [$t(11) = 1.38$, $p > .1$] measures indicated that the rats did not bury either prod significantly more than the other. It should be emphasized that this lack of difference in mean burying between the two sites when the prods were switched reflected the fact that individual subjects were distributing their burying at both sites, not that half the subjects were burying one prod and the remaining half the other. All 10 of the Switch subjects that displayed burying behaviour directed bedding material at both prods. In contrast, only 3 subjects in the Same Condition

Figure 5. Mean duration of burying directed at the shock prod and control prod and the mean height of bedding material at each prod in conditions where the prod positions were switched or left the same after shock.



directed material at both prods [$\chi^2(1) = 10.76$, $p < .005$].

As well as displaying the stereotyped burying pattern described in previous experiments, rats that had been tested with the position of the prods reversed displayed an interesting behaviour not seen in the other rats. Prior to burying the prods, eight of the Switch rats scurried back and forth between the two prods. Moreover, this vacillating behaviour often perseverated into the burying sequence itself, with animals directing bedding material toward one of the prods, then quickly reversing their direction and spraying toward the opposite prod. This is in contrast to the behaviour of the three rats in the Same Condition that directed material at both the shock prod and the control prod; the latter animals did not spray material at the control prod until they had finished burying the shock prod. Similarly, the rats in Experiment 6 that buried both the prod and the hole on the opposite wall did not spray material at the hole until they had buried the prod.

Evidence that position was an important controlling factor was demonstrated by the consequences of changing the position of the prods. Unlike the performance of the subjects in the Same Condition, subjects in the Switch Condition distributed their burying between the two prods. This result also provides evidence that brightness too was exerting control over the burying. If brightness had not been a controlling factor, switching the positions of the two prods, which differed only in brightness, would have been without effect. The results of Experiment 7 thus confirm those of Experiment 6.

Experiment 8

Each of the previous seven experiments provided some evidence that burying can be an adaptive response of rats to specific environmental

threats. Although there can be little question that the response occurs in the presence of aversive stimuli and is directed by specific shock-associated cues, there are other grounds for questioning its adaptive value and consequently its status as a viable defensive response. For example, the stereotyped nature of the response, although facilitating its initial investigation, also raised some questions concerning its adaptiveness in the rat's natural habitat. Such a stereotypical response pattern would be of marginal utility in habitats where available burying materials require more varied responses for their disposition. However, the stereotypical nature of the burying response in previous investigations may simply have reflected the homogeneity of the commercial bedding which served as the only available burying material.

Accordingly, the purpose of the next two experiments was to demonstrate that rats can change their burying responses with respect to the kind (Experiment 8) or disposition (Experiment 9) of available burying materials.

In Experiment 8, each subject was tested in the presence of one of three materials. One of the materials (wooden blocks) was chosen because it would be extremely difficult for a rat to pile this material over the prod using the snout and forepaw pushing motions characteristic of burying in previous experiments.

Method

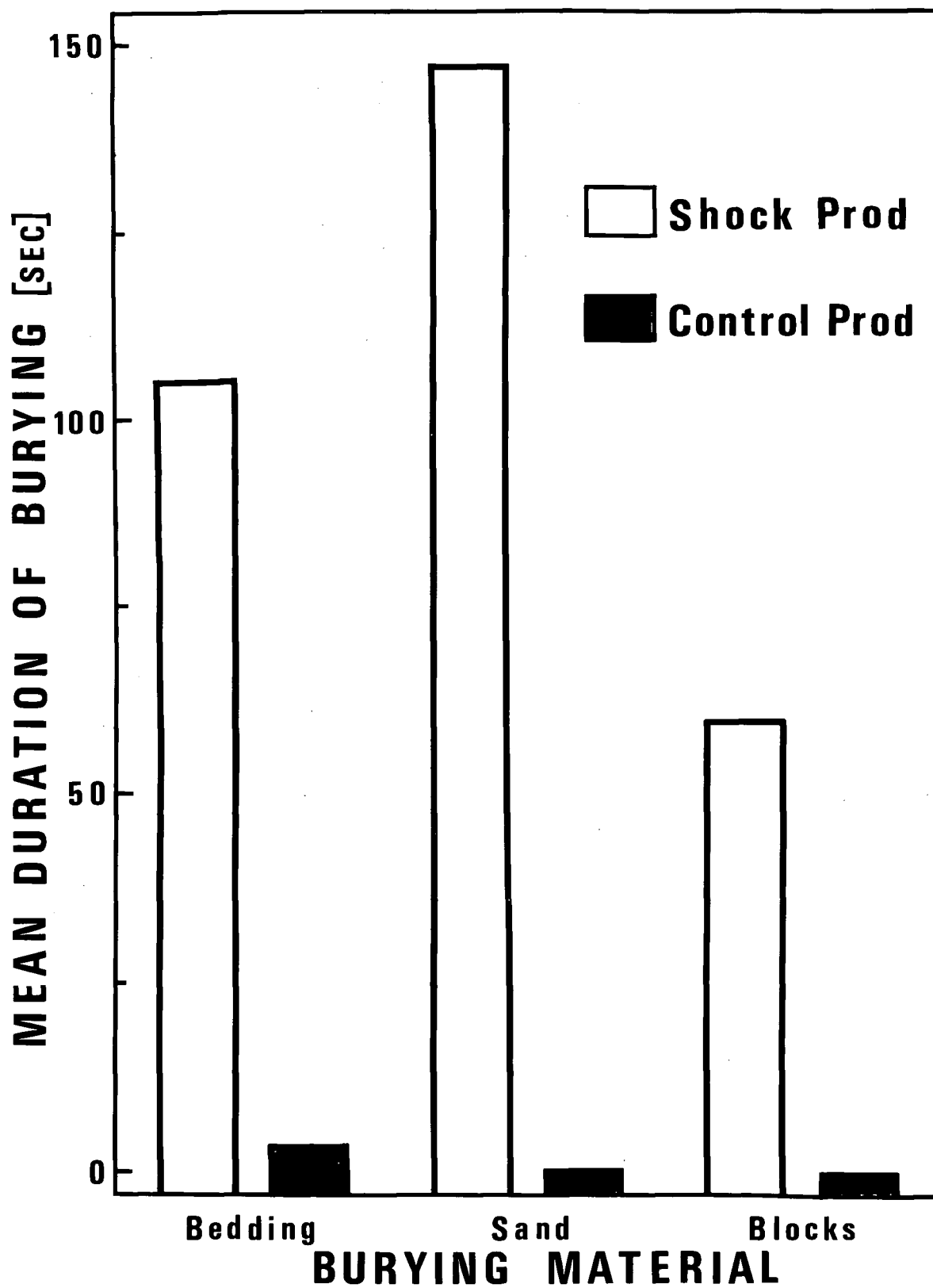
Each of the 30 naive rats was randomly assigned to one of three conditions ($n = 10$). Every subject was treated in the same manner throughout the experiment, except that the type of material available in the test chamber differed for the subjects in each condition. During all phases of the experiment the chamber floor was covered with either (1) 5 cm of San-i-

cel, (2) 5 cm of sand, or (3) 100 24 x 1.6 x 1.0 cm wooden blocks placed so that the height of each was 1 cm. On Day 5, following the usual four days of habituation in the presence of the designated burying material, the subjects were placed individually in the centre of the test chamber between the two identical prods which had been mounted in the middle of the two end walls, 2 cm above the level of the sand or bedding material and 6 cm above the blocks. Each animal was allowed to explore the chamber and to contact each prod at least once without consequence. When the rat next touched one (randomly predetermined) of the two prods, the 8 mA shock was administered. Following the shock, the behaviour of each subject was viewed for 15 min and then the heights of the materials accumulated at the shock and control prods were recorded.

Results and Discussion

Figure 6 shows that the subjects spent a substantial portion of their time burying regardless of which material was available. Only one of the 30 subjects, an animal in the Blocks Condition, did not engage in at least some burying. It is also apparent in Figure 6 that the burying behaviour was well-directed. All 29 of the subjects that engaged in burying spent some time burying the prod which for them had been the source of the shock; whereas, only 3 rats, all in the Bedding Condition, spent any time burying the control prod. Even in these three cases, the subjects spent most of their time burying the shock prod; they did not move material toward the control prod until the shock prod had been completely covered. A priori comparisons (t tests for dependent measures) between the total burying times accumulated by each subject at the respective prods confirmed that the subjects in all three conditions spent significantly more time burying the prod that had been associated with shock (Bedding Condition, $t(9) = 7.83$,

Figure 6. Mean duration of burying the shock and control prod with different burying material.



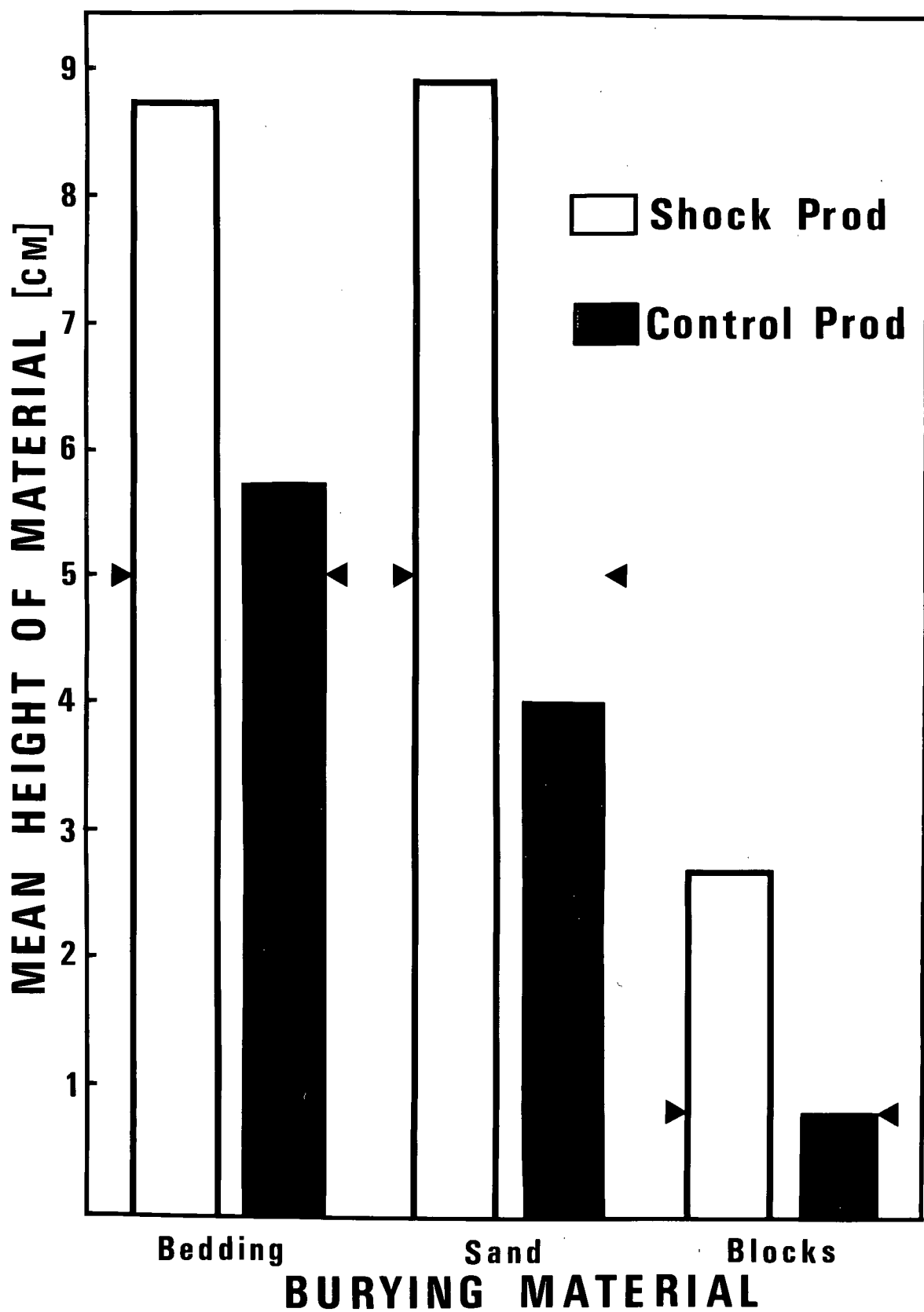
$p < .0002$; Same Condition $t(9) = 6.19$, $p < .0001$; Blocks Condition, $t(9) = 2.75$, $p < .02$).

Analyses of the materials accumulated at each of the two prods (Figure 7) provided an independent confirmation of the behavioural results. In each of the three experimental conditions, the average height of the burying material at the shock prod was significantly greater than that at the control prod (Bedding, Condition, $t(9) = 7.15$, $p < .00005$; Sand Condition, $t(9) = 6.16$, $p < .0001$; Blocks Condition, $t(9) = 2.68$, $p < .02$).

The pattern of burying behaviour displayed by the animals in the Bedding Condition was indistinguishable from that displayed by those in the Sand Condition. In both conditions the topography of the burying response was the same as that observed in previous experiments (see the General Methods). The rats began each burying episode facing the shock prod from a distant part of the chamber. Then they moved directly toward the prod, pushing and spraying the material toward the prod with snout and forepaws. As in previous experiments, these burying sequences were frequently interrupted by intervals of approach-avoidance behaviour in which the rat would stretch forward until fully extended with its nose nearly touching the prod and then abruptly withdraw to the rear of the chamber.

Similar behaviours were also observed in those animals burying with blocks. They would move toward the shock prod pushing blocks ahead of them with snout and forepaws. Although this behaviour was effective in accumulating blocks near the prod, it was necessary for subjects to pick the blocks up in order to form a pile. Seven of the 10 rats that spent some time moving blocks toward the shock prod picked blocks up in their teeth and placed them in a pile with teeth and forepaws. None of these seven managed to completely cover the prod, 6 cm above the original

Figure 7. Mean height of burying materials at the shock and control prods. Arrows indicate the height of the material at the beginning of the test.



level of the blocks, before the end of the test period; whereas, in the other two conditions, in which the prod was closer to the initial level of the burying material, most of the subjects (18 out of 20) actually covered the prod. The rats' behaviour indicated that the construction of the piles of blocks was not haphazard; on several occasions a block just placed on top of a pile toppled to the bottom from where it was quickly retrieved and returned to its original position atop the pile.

The results of Experiment 8 confirm previous demonstrations (Experiments 5 and 7) of discriminated burying behaviour in rats. Every rat shocked by one of two prods mounted on opposite walls of the chamber lined with commercial bedding material returned to the shock prod and buried it, and the few that pushed bedding material at the control prod did not do so until the shock prod had been completely covered. Of greater interest here, however, is the finding that defensive burying is not limited to situations in which there is a supply of commercial bedding material; all of the rats in the Sand Condition attempted to bury the shock prod, as did all but one of the subjects in the Blocks Condition. This finding is consistent with several incidental observations that have been made in our laboratory. In one case, a rat shocked in its home cage dismantled its nest of shredded paper and used it as burying material, and in another case several rats shocked by a prod on the Plexiglas floor of a barren test chamber placed their own feces on top of it.

The results of Experiment 8 also show that burying behaviour is not a reflexive response to objects paired with painful stimulation; rather it is a complex behavioural sequence which varies as a function of the available burying material. In the Blocks Condition, the pushing and

forelimb spraying movements that rapidly produced large piles at the shock prod in the Bedding and Sand Conditions were not sufficient to gain the same end. Such movements were sometimes used to accumulate blocks in the vicinity of the prod, but to construct piles at the prod position, the rats picked the blocks up in their teeth and deposited them around the prod.

These results considered together strengthen the view that burying behaviour could be of considerable adaptive value in natural settings. Rats are capable of using a variety of material to bury objects associated with aversive stimuli even when the use of these materials necessitates changes in the topography of the burying sequence.

Experiment 9

The purpose of Experiment 9 was to demonstrate that rats will attempt to bury a source of aversive stimulation even when all of the burying material has to be transported by the rat to the site.

Method

The subjects were 20 naive hooded rats, habituated to the Plexiglas Chamber in the usual manner, except that the chamber floor was evenly covered with 100, 2.4 x 1.6 x 1.0 cm wooden blocks. Each block was positioned during all phases of the experiment so that its height was 1 cm. On day 5, the subjects were randomly divided into two groups of 10, and shocked by one (randomly predetermined) of the two identical prods. For the subjects in one of the groups, the 100 blocks were distributed on the half of the chamber containing the shock prod; whereas, for subjects in the other group, the blocks were initially restricted to the distal half of the box. The behaviour of each subject and the resulting redistribution

of blocks was measured as in previous experiments.

Results and Discussion

Burying behaviour was again a reliable consequence of the single prod-shock. With the exception of two subjects in the condition where the blocks were adjacent to the shock prod, all of the subjects engaged in at least some burying. Moreover, all 18 of the subjects which displayed the burying behaviour directed it primarily at the shock prod; only two of these 18 moved any blocks toward the control prod. Thus, the subjects spent significantly more time burying the shock prod than they did the control prod in both conditions, when the blocks were adjacent to the shock prod ($M = 36$ and 0 sec, respectively; $t(9) = 2.35$, $p < .04$) and when the blocks were restricted to the far end of the chamber ($M = 108$ and $.7$ sec, respectively; $t(9) = 2.45$, $p < .04$).

These behavioural differences were confirmed by statistical analysis of the height of the piles accumulated at each of the two prods. Because for each subject the initial height of the blocks at the two prods was not equal at the start of the test, the increase in the height of the blocks at each prod rather than the absolute height was used as the index of burying. In both conditions, the average increase in the height of the blocks was 3.7 cm, but in neither condition was there a single instance in which the height of the pile at the control prod was increased (with blocks adjacent to the shock prod, $t(9) = 3.36$, $p < .008$; with blocks restricted to the far end of the chamber, $t(9) = 2.93$, $p < .02$). In contrast to Experiment 8, three subjects, one in the "distal" condition and two in the "adjacent" condition, were able to completely cover the prod with blocks in the 15-min test period.

Between group analyses did not reveal any significant differences between the two groups on either dependent measure (duration of burying shock prod, $t(18) = 1.54$, $p > .10$; height at shock prod, $t(18) = .024$, $p > .10$; duration of burying control prod, $t(18) = 1.48$, $p > .10$; height at control prod, $t(18) = 0$, $p > .10$).

In all previous studies of burying, burying material was always available in the area immediately adjacent to the source of the shock. In Experiment 9 rats attempted to bury the shock prod even when the burying material was initially restricted to the other end of the chamber. After being shocked, the rats carried or pushed the blocks toward the shock-prod for use in its subsequent burial. This observation supports the view that burying can function as an effective defensive response in the rat's natural environment, an environment where burying materials are not always readily available.

GENERAL DISCUSSION

The General Discussion is organized around two issues, that are discussed under separate headings. The first section marshals evidence that suggests that burying is a defensive response of rats. In this regard, both the present experimental data and relevant ethological observations are reviewed. The contribution of the present studies to the "biological" approach to avoidance learning is discussed in the second section of the General Discussion and the relationship of the burying phenomenon to Pavlovian conditioning is examined in this context.

I. Burying as a defensive response in the rat

In each of the nine experiments presented in this thesis, evidence was provided to support the argument that burying behaviour is a prominent defensive response of rats. These data can be organized around the two fundamental criteria: presented in the Introduction: 1) the behaviour must occur in response to aversive stimulation, and 2) it must potentially afford the animal protection from the source of the aversive stimulation.

Experiment 1 provided ample evidence that burying is a prevalent response of rats to aversive shock. Almost all of the rats tested shortly after a single shock attempted to bury the shock source, and even 20 days later the time spent burying was still significantly above control levels. Furthermore, burying was a reliable consequence of prod shock in all subsequent experiments. Perhaps the most convincing demonstration of this effect was provided by the results of Experiment 4 in which increases in the intensity of the aversive stimulus led to increases in the amount of burying. This relationship is consistent with what is known about the relationship between shock intensity and other defensive behaviours (e.g., Ulrich & Azrin,

1962). Even in cases where the type (Experiment 8) and disposition (Experiment 9) of burying materials made the response more difficult to execute, the burying behaviour still occurred in over 80% of shocked animals. The robust nature of the relationship between aversive stimulation and burying behaviour in the present experimental situations appeared to supplant other common defensive behaviours; periods of immobility lasting more than a few seconds, attempts to escape from the apparatus, and aggressive behaviour directed at the prod were rarely observed in the present studies. Evidence of the potential adaptiveness of the response was provided by three different observations. First, the immediate consequence of the behaviour on the surrounding environment in most cases was a "barrier" between the rat and the source of aversive stimulation. This barrier was effective in the laboratory in keeping the rats from making further contacts with a potentially harmful object, and there is no obvious reason to believe that the consequences of this behaviour in more natural aversive settings would not be similar (cf., Calhoun, 1962).

Second, the behaviour was well directed. If burying was randomly directed after aversive stimulation, its adaptive value would be questionable. However, except in those cases where the cues associated with shock had been rearranged between shock and testing (Experiments 6 & 7), few rats were ever observed to push bedding material in any direction other than toward the shock source; the burying seemed to be controlled specifically by the relation between the prod and the shock. Rats shocked through a grid floor (Experiment 3) did not bury the prod, and rats shocked by one prod did not bury an identical prod mounted on the opposite wall of the test chambers (Experiment 5). This latter finding was subsequently replicated in every study in which the two prod procedure was employed (Experiments 7, 8, and 9). However, systematic decreases in the amount of burying were

observed when the brightness or position of the prod was changed in the interval between the shock and the test. These data served as even more compelling evidence that the rats' burying behaviour is guided by the relation between shock and the cues which occasion shock. Thus, this behaviour could have an adaptive value in natural settings; whereas if burying was randomly directed with respect to aversive cues, it would be difficult to imagine how it could be adaptive.

That burying could be adaptive in a natural setting is implied by a third observation, the observation that rats were capable of using a variety of materials to bury the shock prod, even when the use of these materials necessitated changes in the topography of the burying sequence or when materials had to be first transported to the prod. This observation supports the view that burying could be an effective defensive response in the rat's natural environment, an environment where burying materials are not always readily available and where available materials may require a varied response topography for their disposition. Furthermore, this observation shows that burying is not a reflexive response to objects paired with painful stimuli, rather, it is a complex behavioural sequence that can be modified to accommodate different resources of the environment.

Thus, three observations--the physical consequence of the response, the directedness of the response, and the flexibility of the response--suggest that burying behaviour could have adaptive value in a natural setting. However, this evidence only lends plausibility to the argument that burying is adaptive. More direct evidence must come from naturalistic observations in which a positive relationship is demonstrated between instances of the behaviour and the ability of the animal to survive. Showing that the behaviour occurs in a natural environment, although it is not sufficient evidence of adaptiveness, is therefore a necessary step toward direct confirmation

of adaptive value. In this regard, there are a number of more naturalistic observations that extend the present observations.

First, Calhoun (1962) reported that "lower status rats" exposed to "territorial threat" would plug the entrance holes to their underground nests. The notion that "lower status" rodents may 'barricade' themselves away from more dominant members of the species is given further credence by the observation of Johnston (1975). A male golden hamster housed under semi-natural conditions blocked the entrance hole of its chamber with wood shavings after it had been "defeated" by a "higher ranking" male. It is difficult to believe that these 'barriers' could keep burrow-digging rodents at bay. However, the 'signaling function' of these obstructions may be far more important than their effect as physical barriers; specific 'displays' of defeated rodents inhibit further aggression from conspecifics (cf., Blanchard & Blanchard, 1977).

Second, Hudson (1950) observed what he called "pushing of wood shavings" in rats in a passive avoidance situation. Although this behaviour and its relationship to a defensive repertoire were not the focus of experimental scrutiny in Hudson's study, Hudson went on to speculate about its adaptive function in the wild. Although the basis for his speculations was unclear, he asserted that this behaviour was a common response of gophers to traps set in their burrows, and a general response of rodents to reptiles (Hudson, 1950, p. 127).

Hudson's speculations have gained some credibility in the light of the observations of Owings and Coss (1977) and Owings, Borchert, and Virginia (1977). These researchers found that a major part of the ground squirrels behaviour toward snakes was "sand-kicking", and the authors' verbal and pictorial descriptions of the behaviour are nearly identical to the present

description of the responses of the rats in the present studies to prod-shock. That "sand-kicking" was an effective anti-predator behaviour was indicated by the subsequent retreat of the snakes (Owings et al., 1977). In a more systematic laboratory study, a significant correlation was found between sand-kicking and a variety of 'defensive' behaviours of the snakes (Owings & Coss, 1977).

Thus, there is some evidence that 'burying behaviour' occurs in natural situations and that it may have two basic adaptive functions; as a defense against both conspecifics and predators. Since most major naturalistic studies of rodent behaviour (e.g., Calhoun, 1962) have involved populations protected from trapping and predation, it is not surprising that burying has not been frequently reported to be a part of the wild rodent's defensive repertoire.

II. Burying behaviour and a biological approach to aversive learning

The general purpose of the present investigations was to contribute to the development of a 'biological' approach to aversive learning by studying the burying response. Any approach to aversive learning that is based on a knowledge of the animal's natural defensive behaviours will be viewed, for the purposes of this discussion, as a "biological approach". Thus, Bolles' hypothesis is a special case of a biological approach to aversive learning. In general, a biological approach must deal with two, fundamental issues: 1) what the organism's innate defense reactions are, and 2) how the probabilities of these reactions are changed as a result of experience. Accordingly, in the final part of the present discussion, each of these issues is examined in the light of the present data.

Defensive Behaviour

Bolles (1970) has argued convincingly that knowledge of an animal's species-typical defense reactions is essential for understanding its capacity to learn avoidance responses. Bolles, however, did not advocate the empirical study of these defensive behaviours. Instead, on the basis of limited observation, he assumed that rats could respond to novel or dangerous stimuli in only a limited number of ways, i.e., by freezing, fleeing, or fighting. The present data indicate that this assumption is inadequate and that the empirical study of defensive behaviours is essential to any biological account of aversive learning.

Although it seems obvious that the nature of the defensive reactions of organisms should be viewed as an empirical question, this viewpoint raises several problems for a biological approach to aversive learning. For example, Bolles' (1970) hypothesis becomes difficult to apply when it can no longer be assumed that animals display only three defensive behaviours. As the number of potential defensive behaviours increases, the outcomes of studies of aversive learning become more difficult to predict. In addition, many field and laboratory studies would be required to estimate the defensive capacities of even a few, common organisms, and it is unlikely that this behavioural catalogue would be easy to assemble. Even if such a catalogue already existed, it may sometimes be difficult to compare the defensive behaviours that animals display under natural conditions with the behaviour required of them in an experimental setting. For example, 'running away' in a natural situation is not clearly comparable to 'running' in a running wheel, so that it might be difficult to make accurate predictions about laboratory performance that are based solely on a knowledge of

natural defensive behaviours (cf., Schwartz, 1978).

In view of these problems, Bolles' simplifying assumption about the defensive capacities of animals, even if it does not apply in some situations, may appear more attractive than the empirical study of defensive behaviours. The major drawback of Bolles' approach is that it incorporates an assumption that the present data have shown to be unfounded. Furthermore, the present data indicate that the empirical study of defensive reactions can be fruitful, provided that arbitrary experimental constraints on the animal's behaviour are relaxed. Thus, the empirical approach can at least potentially lead to a general biological theory of aversive learning; whereas, an hypothesis that incorporates untested assumptions or assumptions based on limited observations is likely to be successful only within highly restricted settings.

Perhaps a more fundamental assumption on which to base a 'biological' approach to aversive learning is that the defensive behaviours of all animal species have been the product of intense but diverse selection pressures. Indeed, the facts of animal defense appear to be as numerous and diverse as animal species themselves (Maier & Maier, 1970). A first priority of a biological approach therefore might be to order what is already known about animal defense into a coherent base for broad predictions about animal behaviour. It is diversity of this magnitude, not simply the diversity seen in laboratory rats exposed to programmed electric shock, that should be the foundation or "first principle" (Bolles, 1970, p. 34) of a biological account of the diverse phenomena of aversive learning.

The principles of Defensive Learning

The major issue that must be dealt with in any biological approach to aversive learning is how the probability of a defensive response changes

as a result of experience. Bolles (1970) provides two mechanisms to account for changes in response probability. These mechanisms differ depending on whether learning is slow or fast, but in both the consequences of behaviour are emphasized. For fast (SSDR) learning the important consequence is punishing shock, and for slow (non-SSDR) learning it is the production of a reinforcing "safety-signal".

Both of these mechanisms of defensive learning (i.e., reinforcement and punishment) have usually been assumed to apply to any arbitrarily chosen response (see Introduction). Bolles (1970), however, has argued that there are biological limitations on the kinds of responses that animals can learn in 'aversive' situations. Thus, 'general' mechanisms of learning such as reinforcement may not apply to all responses (Bolles, 1972); 1975a). Nevertheless, Bolles must assume that these mechanisms have some generality across responses; otherwise, he would have no basis to expect, for example, that the effects of 'punishment' on freezing behaviour would be comparable to its effects on fleeing. Thus, it may be problematic to argue on the one hand that animals have evolved special responses to dangerous events (SSDRs), while on the other hand invoking learning mechanisms that are assumed to operate in the absence of these "biological constraints".

Although it may turn out that the facts of aversive learning cannot be explained without invoking a number of different learning mechanisms, each having a limited range of applicability, a more parsimonious alternative is a single theoretical framework in which special, nonarbitrary relationships between certain classes of stimuli and responses is a "first principle". I propose that such an alternative can be found within a revived Pavlovian framework, and that a biological approach to aversive

learning might be more readily subsumed by a "classical" Pavlovian learning framework than by the "instrumental" framework evoked by Bolles.

In general, there are two criteria that define Pavlovian conditioning. The first criterion involves an experimental contingency between a 'conditioned' stimulus (CS) to an 'unconditioned' stimulus (UCS). The second criterion is a change in behaviour that results from this operation (Rescorla, 1969).

The Pavlovian conditioning of a defensive response is illustrated in the following example. The presentation of a stimulus that reliably produces a variety of defensive responses (the UCS) is made contingent on the occurrence of a stimulus that is 'neutral' in this regard (the CS). After some number of these contingent CS-UCS presentations, a defensive response begins to occur in the presence of the CS. If it can be shown that the change in the probability of the defensive response is a result of the CS-UCS contingency, then it is a 'conditioned' response (CR).

One advantage of this conceptual framework is that it is consistent with a biological approach to aversive learning. In Pavlovian conditioning, unlike instrumental conditioning, it is acknowledged that the choice of the response to be conditioned is seriously restricted by the type of stimulus used as the UCS. Only if this response is 'nonarbitrarily' related to the UCS (i.e., only if it belongs to the class of responses normally produced by the UCS) will conditioning occur. This kind of biological 'constraint' on learning can be viewed as a more general argument for Bolles' position; i.e., that a response (CR) can be readily learned in an aversive situation only if it is an SSDR (a response produced by the aversive UCS). Bolles,

however, looks past the SSDR to its consequences for an explanation of behaviour change; whereas, a Pavlovian account considers only the stimuli contingently related to the UCS.

A major obstacle to a Pavlovian account of aversive conditioning is represented by a traditional distinction (e.g., Skinner, 1938) between instrumental and classical conditioning. The idea is that instrumental conditioning controls all skeletal, or voluntary responses; whereas, classical conditioning controls autonomic, 'involuntary' responses. If this were true, then it would be difficult to argue that a skeletal defensive response such as running could be classically conditioned. The fact is, however, that autonomic responses such as heart rate apparently can be instrumentally conditioned (e.g., DiCarra & Miller, 1968) and directed skeletal responses such as key pecks can be classically conditioned (e.g., Brown & Jenkins, 1968). The latter effect has been called "autoshaping" or "sign tracking" and its relationship to the results of the present studies will now be discussed.

Until 1968, the pigeon's key peck was considered the prime example of 'voluntary' behaviour controlled by its consequences. However, Brown & Jenkins (1968) began an area of research that has led to the current view (e.g., Schwartz & Gamzu, 1977) that the key peck may be in large measure a respondent behaviour under Pavlovian control. In Brown & Jenkins' paired access to grain with a lit key, in spite of the absence of any formal contingency between the pigeon's behaviour and access to food, after a few trials of these CS-UCS pairings, pigeons began to peck the key. Two kinds of evi-

dence suggested that this "autoshaping" phenomenon was due to Pavlovian conditioning. First, as in all instances of Pavlovian conditioning, the contingency between the CS and the UCS was critical for the emergence of the behaviour (e.g., Brown & Jenkins, 1968; Gamzu & Williams, 1971). Second, and perhaps most importantly, autoshaped key pecks persisted even when there was a negative instrumental contingency between key pecking and access to grain (Williams & Williams, 1969). It is very difficult to explain in instrumental terms why the only response that was not followed by food should gain in strength.

The Pavlovian conditioning of directed skeletal responses (Hearst, 1975) has been part of what Bolles (1975a) has called a "revolution" in behaviour theory; the straightforward idea that 'operant behaviour' can be analyzed mainly in terms of its consequences has received a serious challenge from the autoshaping data (Schwartz & Gamzu, 1977). However, in spite of the intensive study that this phenomenon has received over the past ten years (for reviews, see Hearst & Jenkins, 1974; Hearst, 1975; Schwartz & Gamzu, 1977), its generality has been limited by the fact that there are no clear instances of autoshaping with an aversive reinforcer.

The purpose of the final part of this discussion is to briefly marshal evidence that suggests that much of the behaviour described in the present thesis may represent the Pavlovian conditioning of a directed defensive reaction (i.e., a type of autoshaping). The validity of this argument has implications for both the generality of the autoshaping phenomenon and the feasibility of a Pavlovian interpretation of defensive learning.

A questionable example was provided by Rach (1969). The conditioning of aggressive responses in *Betta splendens* (Murray, 1973) may represent an exception to this generalization.

In the following table, several features of autoshaping and defensive burying are directly compared.

| <u>Autoshaping</u> | <u>Defensive Burying</u> |
|---|---|
| 1. a high percentage of subjects exposed to a contingency between a key (CS) and food access (UCS) learn to approach the cue and 'peck' it (CR) | a high percentage of subjects exposed to a contingency between a prod (CS) and shock (UCS) learn to approach the shock source and bury it (CR) |
| 2. Autoshaped behaviour is not a simple 'reflex' elicited by cues associated with food; it is a directed, skeletal response. | Burying behaviour is not a simple 'reflex' elicited by cues associated with shock; it is a directed, skeletal response. |
| 3. Autoshaping occurs in the absence of an instrumental contingency between food and pecking; furthermore, the first instance of a behaviour (e.g., key peck) cannot be explained by its consequences. | Burying behaviour occurs in the absence of an instrumental contingency between itself and shock; furthermore, the first instance of a behaviour cannot be explained by its consequence. |
| 4. A positive correlation between the occurrence of the CS and the UCS is mainly responsible for the first approach and peck at the CS. Common controls for Pavlovian conditioning (i.e., CS alone, UCS alone, discriminative conditioning) yielded results expected for a Pavlovian learning process. Animals directed their behaviour toward cues positively correlated with the UCS. | A positive correlation between the prod (CS) and the shock (UCS) appears to be responsible for approach to and burying of the CS. (Exps. 1-9). Common controls for Pavlovian conditioning (i.e., CS alone (Exps. 1, 4, 6), UCS alone, (Exp. 3), discriminative conditioning (Exps. 5, 7, 8, 9) generally yielded results expected for a Pavlovian learning process. Rats directed their behaviour toward cues positively correlated with the UCS. |
| 5. Approach to and contact with the CS will persist even when there is a 'negative' instrumental contingency between pecks and food delivery. | Approach to and burying of the CS occurs despite a prior, implicit punishment contingency between approach and shock. |
| 6. Exposure to the CS-UCS contingency itself is sufficient for the later appearance of the CR. Key-pecking does not have to occur during the CS-UCS pairing. | Exposure to the CS-UCS contingency itself is sufficient for the later appearance of the CR. Burying does not have to occur during the CS-UCS pairing. |

Although these similarities between autoshaping and burying are provocative, the differences between these phenomena are of equal theoretical importance. One difference is that the autoshaped response takes about 50 trials to establish (Hearst, 1975), whereas the burying response occurs after only one 'trial'. Two considerations may make these differences comprehensible. The first consideration is survival. Animals in their natural environment do not have much time to learn about dangerous things. The last trial of aversive learning for the prey is the first trial of appetitive learning for the predator. In order to facilitate survival, the defensive learning of the prey must be quick and effective (Bolles, 1970). An organism equipped with this kind of defensive capacity would have a selective advantage that may be transmitted to later generations. On the other hand, the appetitive learning of an animal like the pigeon, although just as essential for survival, can generally follow a longer time course without ill effect. In other words, selection pressure for rapid appetitive learning in the pigeon may be less than that for rapid defensive learning in the rat. Although evolutionary considerations such as these are difficult to evaluate directly, they may lead to interesting predictions about comparative animal learning (cf., Bolles, 1975a).

A second consideration that may account for the difference between the acquisition rates of Pavlovian key pecks and conditioned burying is one that is more accessible to experimental test but which has not received much attention. It is a natural complement of temporal contiguity (Pavlov, 1927) that may turn out to be just as important: spatial contiguity of the CS and the UCS. The burying paradigm is unusual in that the UCS (shock) is delivered through a well-defined, localized CS (prod). Because noxious

stimuli in the animal's natural environment are usually spatially contiguous with the cues that signal their occurrence, it is not unreasonable to assume that laboratory animals may be able to learn about spatially contiguous events more easily than those that are not. The hypothesis is certainly worth testing, both in the case of the pigeon's autoshaped key peck and in the case of the rat's conditioned burying response.

A second apparent difference between autoshaping and the burying phenomenon concerns the nature of the relationship between the CR and the 'unconditioned' response (UCR) to the UCS. The pigeon's conditioned key peck, although not the same as its unconditioned response to food, is very similar, (Jenkins & Moore, 1973). Likewise, several other instances of Pavlovian conditioning are consistent with the notion of stimulus-substitution: i.e., the subject acts in the same way toward the CS as it does toward the UCS. Clearly, burying is a different response from those initially elicited by shock (e.g., withdrawal).

It is important to remember that stimulus substitution is a theory about the mechanism of Pavlovian conditioning. There is nothing in the data on Pavlovian conditioning that suggests that all CRs are the same as the UCRs elicited by the UCS. In fact, there are many examples of Pavlovian CRs that are not the same as the UCR. Obrist, Sutterer, and Howard (1972) showed that an unconditioned response to electric shock was invariably cardiac acceleration; however, when shock was paired with a CS in the usual Pavlovian manner, the CS later elicited cardiac deceleration. This CR was

adaptive in the sense that it may have prepared the animal for impending cardiovascular strain, but it was the opposite of the unconditioned response to shock. Siegel (1972) injected insulin into rats on a fixed schedule. The unconditioned effect of insulin was to lower blood sugar. When rats were later tested with the CS alone (saline injection), their 'conditioned' response was an increase rather than a decrease in blood sugar. Again, the CR did not fit the theory of stimulus substitution but it was clearly adaptive. Alternatively, if the UCS is glucose, the CR is not an increase in blood sugar but a decrease (Deutsch, 1974). When the UCS is morphine, the CR is not reduced pain sensitivity; it is increased pain sensitivity (Siegel, 1975, 1977). Other instances of discontinuities between CRs and UCRs can be found in the autoshaping literature. For example, Wasserman (1973) found that baby chicks pecked at a key predicting four seconds of heat, but they did not peck during heat. Grant (1974) showed that responses toward a conspecific CS were dissimilar to those elicited by the food UCS. In this instance, 'social grooming' was the dominant CR.

Thus, it may be premature to reject the notion of a Pavlovian conditioned burying response on the grounds that it is dissimilar to the unconditioned response to shock, or because the acquisition of this response takes place in one 'trial' while the acquisition of other conditioned responses usually requires many more trials. On the other hand, the idea of a conditioned burying response gains some credibility because of several, striking similarities between burying behaviour and autoshaping, a phenomenon that has commonly been interpreted as an instance of Pavlovian conditioning. The most important similarities are 1) that both are directed, skeletal responses, 2) that neither phenomenon can be readily explained by

instrumental contingencies, and 3) that in both cases a Pavlovian contingency between a CS and a UCS seems to be critical for the emergence of the behaviour. Although the present studies of defensive burying were not designed with this comparison in mind, they do provide some data that are consistent with the argument that burying behaviour may also represent the Pavlovian conditioning of a directed skeletal response.

The ~~proof~~ of this argument would extend the generality of the auto-shaping phenomenon, and provide substance to the "alternative" biological approach to aversive learning being presented here. According to this view, species-typical defense reactions such as running or freezing are directed by Pavlovian rather than instrumental contingencies in the organism's environment. Thus, the successful prediction of defensive learning must be based on a thorough knowledge of the organism's 'unconditioned' defensive repertoire, and on a careful analysis of the Pavlovian contingencies that act on this repertoire. Study of the burying phenomenon may serve as a natural starting point for the development of such a biological approach to aversive learning.

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