

AN INVESTIGATION OF RODENTS' USE OF LEARNED CALORIC INFORMATION
IN DIET SELECTION AND FORAGING

by

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Abstract

When given a choice between two foods of equal caloric value but different flavors, rats show a robust preference for that food whose flavor was previously associated with a higher calorie food. This finding suggests that rodents may identify food quality by sensory signals such as taste. The first portion of this thesis explores this flavor-calorie conditioning effect in other rodents, namely hamsters and gerbils. When hamsters were tested in the same paradigm as rats, the conditioning effect was not observed. This discrepancy may have resulted from the hamsters' ability to store food mash in their cheekpouches. Accordingly, hamsters were next presented with liquid diets which could not be cheekpouched. The conditioning effect was observed when different flavors were associated with different quality liquid diets. However, the effect was less robust than that discovered for rats. A second species, gerbils, did show robust conditioning effects. Thus, unlike rats and gerbils who show a robust flavor-calorie conditioning effect, hamsters are less likely to identify food quality by using taste cues.

Once conditioned to detect caloric density by using flavor cues, hamsters and gerbils were placed on an 8-arm radial maze that consisted of four arms baited with high-calorie liquid and four arms baited with low-calorie liquid. The purpose of this second part of the thesis research was to investigate the rodents' preference for food locations that contained food of varying qualities. Both species were expected to visit and

drink first from the arm locations containing the higher calorie liquid. Although hamsters did not visit more high-calorie arm locations, they did drink from these arms more often. When visiting arm locations, hamsters appeared to use a circling strategy that began in the same arm each trial and consisted of visits to consecutive arms. Gerbils neither visited nor drank more often from the high-calorie arm locations. Gerbils also did not appear to use a circling strategy. Thus, when foraging on an 8-arm radial maze for food of varying quality, hamsters' use of a circling strategy prohibited them from first visiting high-calorie arms but not from preferentially drinking from these locations. Unlike hamsters, gerbils did not adopt a strategy to collect food rewards and were not selective about the food reward that was consumed.

The foraging strategies of hamsters was further explored in the third part of the thesis. Hamsters were allowed to forage on an equally-baited 17-arm radial maze. Each arm location was baited with a sunflower seed. Once again, hamsters visited arm locations by using a circling strategy which consisted of visits to consecutive arms. However, on the larger maze hamsters did not begin each trial in the same arm location. In addition, hamsters that were placed on the same maze with 4 of the 17 baited arms blocked, given 13 arm location choices, removed from the maze while the blocks were also removed, and placed back on the maze to select 4 additional arm locations, did not preferentially select the previously blocked arms. Thus, hamsters whose response algorithm was disrupted did not show a

memory-based strategy for collecting seeds from the maze.

The major conclusions from this research are that 1.) Hamsters can learn to associate caloric density and flavor cues, but the learned effect is easily extinguished. 2.) This dietary information may be used when deciding what to eat but not where to forage. 3.) Hamsters appear to be harvesters who visit all foraging locations by adopting a response strategy. 4.) Gerbils can also learn to associate caloric density and flavor, and the learned effect is robust. 5.) Gerbils do not appear to use this information when deciding which foods to eat or where to forage. It will be interesting for future studies to see if rats use flavor-calorie information in foraging settings.

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I. INTRODUCTION

At some point, generalist foragers whose diet, unlike that of a specialist, consists of several food items must decide which foods to eat. Omnivorous central place foragers such as hamsters and squirrels may decide which foods to eat before or during a foraging bout, or after return to its home. According to Optimal Foraging Theory (OFT) (cf. Emlen, 1966; Hughes & Townsend, 1981; Krebs, Houston, & Charnov, 1981; Krebs, Stephens, & Sutherland, 1983; Pyke, Pulliam, & Charnov, 1977), foragers select food in a manner that maximizes benefits and minimizes costs. The most commonly used currency representing costs and benefits is energy measured in terms of caloric units (Schoener, 1971). Thus, animals are viewed as foraging optimally if their caloric input outweighs their caloric output (e.g., travel expenses, handling of food, etc.). Foragers, especially generalists, often remain flexible allowing different foods to be selected while maintaining the same energy balance or caloric intake.

The assumption that foragers essentially regulate or balance energy by means of caloric ingestion is a simplification. It may be more realistic to define an optimal food choice by a forager as a decision that grants the greatest nutritional benefit while inflicting the least cost. Nutritional requirements involve more than caloric intake. Foragers must also regulate the amount of mineral and vitamin intake as well as avoid toxic substances. The rats' ability to recover from a vitamin-deficient or mineral-deficient diet by

selecting foods which provide recovery is well known (Adam, 1973; Handal, 1965; Harris, Clay, Hargreaves, & Ward, 1933; Rozin, 1967; Zahorik, Maier, & Pies, 1974). The rats' ability to avoid toxic compounds has also been widely demonstrated (Galef & Clark, 1971; Barnett, Cowan, Radford, & Prakash, 1975; Garcia, Rusiniak, & Brett, 1978, Melcer & Timberlake, 1985). Although the regulation of energy balance seems to predominate over other essentials, in that, rats as an example will not overeat calories in order to obtain adequate amounts of protein (Andik, Donhoffer, Farkas, & Schmidt, 1963) or water (Bruce & Kennedy, 1951), not all foragers appear as optimal calorie gatherers (Giraldeau & Kramer, 1982; Lobel & Ogden, 1981; Milton, 1979; Pulliam, 1980; Rapport, 1980; Tinbergen, 1981; Vadas, 1977).

The energy maximizing model of optimal foraging assumes that animals aim to maximize net intake (i.e., calories) with no nutritional constraints, with perfect knowledge of food quality and of tradeoffs with other kinds of costs or benefits (Krebs, Stephens, & Sutherland, 1983). However, in most instances, to assume that maximizing gain in terms of energy is an appropriate optimization criterion is an error. Giraldeau and Kramer (1982), for example, found that load size of chipmunks carrying seeds back to a central cache was consistently smaller than predicted by an energy maximizing model. The incongruity of empirical findings and the energy maximizing model may be a result of a foragers' need to establish a tradeoff among caloric balance, toxin avoidance, and

non-caloric nutritional requirements when deciding which foods to eat.

The penalty for failing to maintain a proper diet as well as avoid toxic substances can be deleterious or even fatal. For instance, ingesting a toxic substance can result in sickness or death. A sick animal is at heightened risk if unable to escape predators when foraging, and at a disadvantage if unable to transport food to its home. Although the body has elaborate internal mechanisms such as poison detoxification, nutrient biosynthesis, and nutrient storage to avoid the danger of eating something harmful or eating too much of a 'good' food, animals' behavior also plays an important role in regulating nutritional balance. Recent studies suggest three behavioral mechanisms that an animal may use in diet selection. These are innate preference, social transmission, and experience-based acquisition of dietary information.

An innate preference in food selection is illustrated by animals' preference for sweet-tasting food items (Rozin, 1976). Sweet-tasting food items represent foods with a high sugar content. In light of OFT, choosing foods with a high sugar content and therefore high caloric content maximizes energetic intake. Accordingly, a greater benefit is derived from increasing caloric input by ingestion of sweet foods than from ingesting a more abundant food with less sugar per food item. However, all behavior cannot be explained by such innate mechanisms. Evidence exists for other cost-reducing mechanisms of diet selection.

Social transmission is a cost-reducing mechanism of diet selection that allows an animal to benefit from watching the feeding behaviors of others. Galef (1984) has shown that under a wide variety of experimental conditions, an 'observer' rat will adopt the diet of a 'demonstrator' rat. This includes rats that are wild and domesticated, food deprived and non-food deprived, with familiar and unfamiliar partners, liquid-drinking and mash-eating, as well as young and old. However, most examples of social transmission consider juveniles' gathering of information about food quality from watching parents food choice (Galef & Sherry, 1973; Hogan, 1977). For example, Galef and Clarke (1972) describe the transmission of diet preference patterns from mother rat to pup. This transmission occurs via two possible routes. First, rat pups may feed in the environment along with their mother, become familiar with certain foods, and prefer these familiar foods after weaning (Galef & Clarke, 1971, 1972). Second, information about diet quality may be passed along to the pup via the mother's milk (Galef & Henderson, 1972; Galef & Sherry, 1973; LeMagen & Tallon, 1966). By noting which foods are ingested, juveniles can avoid toxic foods and minimize the amount of sampling necessary in developing an adequate diet. We must remember that illness as a result of poisoning increases the amount of energy the body needs for recovery while inhibiting the sick animal from gathering more food. Thus, social transmission reduces the costs of deciding which foods to eat.

Experience-based acquisition of dietary information occurs

when an animal associates a sensory attribute of the food with dietary quality. The Blue jay's strong avoidance response to the toxic monarch butterfly and its non-toxic mimic, the viceroy butterfly, after ingestion of the toxic monarch butterfly (Brower, 1958) is a good example that involves a visual stimulus. Booth (1972) has demonstrated the rats' adjustment in meal size using olfactory stimulus cues as a determinant of caloric density. Rats ate less of a daily meal if the odor associated with the meal had previously been paired with a high-carbohydrate diet. This, too, is an example of an experience-based diet modification. As opposed to innate preference and social transmission, food selection by this means involves a feedback system based upon trial and error. That is, an animal samples a new food, if the food item is beneficial he continues to ingest the food item, if not he avoids ingestion. An important question, however, is what is the basis for judgement when comparing good and better foods. Avoiding a food that produces illness is a clearcut distinction between a good and bad food. But, what distinction can be used to choose between adequate and better foods?

When animals choose food, we label the selected food as the preferred food. If all members of the same species choose the same food upon initial presentation, then we conclude that the animal has an innate preference for that food. If the likelihood of choosing a food changes due to the animals' experience with that food, we conclude that the animal has a learned preference for that food. Preferences are learned when

ingestion of a substance is followed by an improvement in 'physiological state' (Garcia, Hankins, Rusiniak, 1974; Revusky, 1967; Zahorik and Maier, 1969). Evidence for poison avoidance (good vs bad) suggests that animals learn to avoid toxic substances quickly and maintain this avoidance behavior for long periods of time (Riley & Clarke, 1977). However, the sparse evidence for learning about the positive aspects of foods and the flavors associated with them suggests that animals require long-term experience with the food, and that the behavior which is learned is quickly extinguished (Mehiel & Bolles, 1984). Thus, a difference in preference for adequate vs better foods is harder to detect than a difference in preference for good vs bad foods.

Three studies have demonstrated rat's preference for familiar-beneficial foods (better) over familiar-safe foods (adequate). In 1967, Revusky measured the effects of deprivation using a preference technique. Rats were conditioned to prefer either grape juice or milk depending upon which liquid they had access to when deprived. For instance, rats in a first group were fed grape juice while hungry and milk while satiated, and rats in a second group recieved the opposite treatment. In a subsequent test choice, the first group preferred grape juice more than the second group. Revusky concluded that the rats' preference for a food was greater if the food had previously been consumed at a high deprivation level than at a low deprivation level regardless of the test deprivaton. Thus, rats preferred the familiar-beneficial food. In 1974, Zahorik,

Maier, and Pies compared the thiamine-deficient rats' preference between a recovery flavor (better) and a familiar-safe food (adequate). Four groups had a distinctive flavor paired with a certain phase of the experiment. That is, flavors were presented either before the rats became thiamine deficient (old-familiar flavor); while the rat received thiamine injections during the recovery period (recovery flavor); after the last recovery injection (new-familiar flavor); or for the first time during the test phase (novel flavor). When given a choice between the recovery flavor and the familiar-safe flavor or novel flavor rats who were no longer thiamine-deficient preferred the recovery flavor. Thus, they also preferred the familiar-beneficial food.

More recently, Bolles, Hayward, and Crandall (1981) reported the rats' preference for tastes associated with higher calorie food items. Bolles et al. (1981) gave two groups of rats several trials in order to form an association between the flavor of a food mash and its caloric density. Rats were given two foods in their homecages. A high-calorie food mash had one flavor. A low-calorie food mash had a second flavor. The caloric density - flavor association was counterbalanced. Once the rats consumed more high-calorie food mash, they were allowed to choose between the two flavors when the food mashes were of equal caloric content. The rats more often chose the flavor previously associated with the high calorie mash. Their choice of mash was reliable and consistent with their knowledge of flavor as a mediating cue to caloric density. In addition to

demonstrating a robust effect, Bolles et al. developed a procedure amenable to testing other rodent populations.

The role of conditioning in diet selection is explored further in this thesis. In particular, the rodents' use of caloric density information is investigated. Golden hamsters (Mesocricetus auratus) and Mongolian gerbils (Meriones unguiculatus) were given a choice between a good food of adequate caloric value and a better food of higher caloric value. Bolles et al. (1981) demonstrated the effect that prior conditioning of flavor cues to caloric density has on a rat's ability to choose a high-calorie food item. Thus, the first portion of this thesis is simply an extension of Bolles et al.'s work to examine the conditioning effect in other rodent species.

There is also a second focus in this thesis. If rodents can choose nutrient rich sources by its associated flavor and will use this information as a basis for future decisions when encountering the same flavor, then will rodents use this information in actual foraging situations? That is, we asked if the addition of cost of travel to our original two choice procedure would change the rodent's decision to consume high calorie foods.

Traditionally, the effect of travel on rodents' foraging has been analyzed in a radial-arm maze situation. A radial-arm maze consists of a central hub with a number of arms or alleys radiating away from the central area. Typically, food or water is placed at the end of each arm. Then, animals who are food or water deprived must locate or collect the reward. For example,

Batson, Best, Phillips, Patel, and Gilleland (1986) examined rats' preference for certain arms when water and/or food deprived. They report that rats are able to alter their preference for a radial maze arm which is empty, is associated with a toxic substance, or contains a high quality food source. An arm was preferred when chosen at the beginning in a sequence of eight choices. Thirsty rats who foraged for water rewards on an 8-arm radial maze decreased their preference for an empty arm. Rats that learned a saccharin-lithium association either on the maze or in their homecage decreased their preference for an arm containing saccharin. When food and water deprived, rats increased their preference for an arm containing a sweet chocolate milk solution. Thus, Bateson et al. illustrated the rats' ability to alter their preference for a food site (arm location) when nutritional needs changed or the quality of the food item changed.

In the second set of studies reported in this thesis, both gerbils and hamsters were placed within a foraging situation on an 8-arm radial maze where one-half of the arms were baited with a high-calorie liquid and one-half with a low-calorie liquid. Although, I expect the rodents to first visit those arms baited with the high-calorie liquid, this may not be the case.

A secondary purpose of this thesis was to examine the foraging strategy of hamsters in the radial-arm maze. The foraging strategies that are observed in a radial-arm maze situation vary among species. Since Olton, Collison, and Werz's (1977) investigation of the radial maze performance of rats, at

least six other species have been tested in the radial-arm maze. These are Mongolian gerbils (Meriones unguiculatus) (Wilkie & Slobin, 1983), CD-1 mice (Mus) (Mizumori, Rosenzweig, & Kermisch, 1982), ring doves (Streptopelia risoria) (Wilkie, Spetch, & Chew, 1981), domestic pigeons (Columba livia) (Bond, Cook, & Lamb, 1981; Roberts & Van Veldhuizen, 1985; Spetch & Edwards, 1986), Savannah sparrows (Passerculus sandwichensis) (Moore & Osadchuk, 1982), and Siamese fighting fish (Betta splendens) (Roitblat, Tham, & Golub, 1982).

A foraging strategy can be characterized as either a response strategy based on algorithmic responding or a memory-based strategy relying on environmental cues. One response strategy is to visit successive arms in a choice sequence in a clockwise (+) or anti-clockwise (-) direction (Foreman, 1985). For instance, a subject may visit each arm (+1), or skip two arms and visit the arm which is three arms away from the last choice (+3). We look for response patterns by showing the frequency of selection (e.g., 20 visits) dependent upon the number of arms distance from the arm just visited (e.g. +1). A distribution that is peaked and unimodal illustrates algorithmic responding. If the peak is + or -1, then the subject visits each arm consecutively. The consecutive arm pattern (+ or -1) is usually seen on large mazes (Olton & Werz, 1978). An algorithm is not considered as evidence for spatial memory because choice is independent of food location (Eckerman, 1980). Siamese fighting fish use of a response strategy when foraging on the radial-arm maze is a good example (Bond, Cook, & Lamb,

1981).

Rats and gerbils, on the other hand, perform more effeciently on the radial-arm maze and may use a memory-based strategy (cf. Olton, 1978; Roberts, 1984). The rats' ability to avoid entering unbaited arms seems to be controlled by extramaze visual cues that distinguish various locations (Olton & Collison, 1979; Zoldeck & Roberts, 1978). Also, the order of selections varies from trial to trial and subject to subject, implying that accurate performance is not simply a result of learning a particular route through the maze (Olton & Samuelson, 1976). However, rats foraging on the radial-arm maze have also been known to use a response strategy (Foreman, 1985; Yoerg & Kamil, 1982). Response patterning appears to complement rather than replace the rats' use of a spatial representation of the environment. The rats' use of either a response or memory-based strategy was largely determined by the task procedure employed by the experimenter.

Ring doves (Wilkie & Slobin, 1983) and pigeons (Roberts & Van Veldhuizen, 1985) will also display accurate working spatial memory when given special and extended training on the traditional radial-arm maze. Savannah sparrows also perform accurately when tested outdoors in an 8-arm radial maze (Moore & Osadchuck). For pigeons, demonstration of a working spatial memory is a recent discovery. Bond, Cook, and Lamb (1981) compared the performance of rats and pigeons on the same 8-arm radial maze and found lower accuracy in the pigeons. They suggested that the pigeons' performance was a result of having

been forced to feed in an unnatural setting. Accordingly, Spetch and Edwards (1986) allowed pigeons to feed in open-field environments with eight elevated food sites. In this more naturalistic setting, pigeons displayed evidence of working spatial memory within a few trials. The pigeons' use of a foraging strategy, like that of the rat, seems to depend upon the task procedure employed by the experimenter.

Mice, unlike rats and pigeons, foraging on a radial-arm maze gave no evidence of improved performance beyond that exhibited during the first few days of training (Mizumori, Rosenzweig, & Kermisch, 1982). Although mice did choose baited arms at accuracy levels above chance, Mizumori et al. concluded that their performance called forth the need to question the use of radial-arm mazes as an indicator of innate food-search behaviors. In particular, Mizumori et al. stated that other species' performance on the radial-arm maze should be explored in order to investigate the comparability of food-search behaviors in the field, variables that affect search behaviors, and how these factors directly influence radial-arm maze performance.

The foraging strategy of another commonly studied rodent - the hamster - on a radial-arm maze is unexplored. Thus, in a final study, hamsters were allowed to forage on a radial maze where arms were baited equally with a single sunflower seed. This study served two purposes. First, the hamsters' performance can be compared to other species. Second, the hamsters' performance can be compared to hamsters' performance

in a maze which is unequally baited (viz. Experiment 2).

II. EXPERIMENT 1

The purpose of Experiment 1 was to replicate Bolles et al. (1981) in order to test the robustness and uniformity of the flavor-calorie conditioning phenomenon across species. Golden hamsters and Mongolian gerbils were given experience with two diets, one high in calories and one low in calories. Each diet was marked by a distinctive flavor. Diets were either liquid or a mash. The conditioning of flavor preferences was assessed by the degree to which subjects preferred the high-calorie flavor in a choice test in which the two flavors were placed in diets of isocaloric densities.

Experiment 1 consists of three parts: mash preference of hamsters, liquid preference of hamsters, and mash preference of gerbils.

1. PART 1

1.1 Method

1.1.1 Subjects

Sixteen experimentally naive Golden hamsters (Mesocricetus auratus) (eight female, eight male) were individually housed in wire mesh cages (24 cm x 18 cm x 17 cm) on a reversed 12-hr light/ 12-hr dark cycle (dark cycle began at 8:00 a.m.). They were tested during the last third of the dark cycle. They had unlimited access to water.

1.1.2 Materials

During the conditioning phase, a subject was given access in its homecage to a single 2.5 cm tall paper cup that contained a flavored mash. The cup was glued to a 13 cm x 8 cm x 5 cm wooden base.

During the test phase, a subject was given access in its homecage to two cups that contained flavored mash. The cups were glued to a 13 cm x 8 cm x 5 cm wooden base and separated by a 5 cm x 5 cm wooden partition.

The high-calorie mash consisted of the following: 100 g Canadian corn starch (Best Foods), 13 g generic vegetable oil, 38.5 g Purina lab chow, 10 g flavor, and 100 ml water. This mixture was about 5.0 calories per gram. The low-calorie mash contained no starch. Calories were reduced by substituting alpha-cellulose fiber for starch. Alpha-cellulose fiber is indigestible and therefore has no calories. Thus, the low-calorie mash consisted of the following: 100 g alpha-cellulose fiber (National Biochemical Corp.), 13 g generic vegetable oil, 38.5 g Purina lab chow, 10 g flavor, and 100 ml water. This mixture was about 1.0 calories per gram. Flavors were provided by adding to the diets raspberry and strawberry extract (Club House). Body weights and food mash weights were measured to the nearest gram by using a standard laboratory scale.

1.1.3 Procedure

On conditioning days, the subjects had ad lib access to water and a single flavored mash. The subjects were presented with 30 g of high- or low-calorie mash on alternate days. Each diet was flavored with either raspberry or strawberry. For eight subjects (four female, four male) raspberry flavoring was added to the high-calorie diet and strawberry to the low-calorie diet. The flavors were reversed for the other eight subjects. Consumption was measured at the end of each 24-hr period. (Pilot studies suggested that spillage was negligible; consequently, this method of measuring consumption was possible.) On the third day, the test food was replaced by standard laboratory chow in order to ensure that proper nutrient requirements were maintained. The fourth day was a deprivation day when neither test food nor laboratory chow was available. This cycle was repeated four times prior to the test phase. Although Bolles et al. only repeated the cycle twice prior to the test phase, preliminary studies suggested that hamsters were not as readily conditioned to taste cues as rats.

On test days, the subjects were offered two cups of food, but at this time the food in both cups was the same, consisting of a mixture of equal proportions of the high- and low-calorie diets. The only difference between the two test diets was the addition of the flavors that had previously been correlated with caloric density. During the first 5 min of testing, subjects were tested in groups of two so that the experimenter could record the amount of time spent eating, sniffing or transporting

the contents of each cup. Eating is defined as the actual consumption of mash or the act of putting mash into the cheekpouch. Sniffing is noted when the subject stands on his hind legs over the mash. Being next to the food cups on all four paws is not considered as sniffing. A measure of transporting was included because subjects transported either the food cups or cheekpouch contents to the corner of the cage where they stored their food. The amount of time spent engaged in at least one of these activities was tracked on a stopwatch. Accordingly, the total measure was a composite of the amount of time spent eating, sniffing, or transporting mash. Consumption of mash was measured after the first hour and again after 24 hr. The diet that was visited first was also recorded. After the first test day, all subjects spent the next 24 hr with ad lib access to laboratory chow. This was followed by a 24-hr deprivation period. After this deprivation day, a second test day identical to the first occurred.

1.1.4 Statistics

When analyzing measures of mash and liquid consumption or time spent eating, sniffing, and transporting mash during the first 5 min of observation, a within-group analysis of variance with two fixed factors, trial and caloric density (high or low), was used. An interaction between the amount of mash or liquid consumed per trial and caloric density demonstrates the conditioning effect. That is, conditioning occurs when an increase in high-calorie consumption is coupled with a decrease in low-calorie consumption. Extinction produces the opposite

effect. In order to conclude that conditioning or extinction has occurred the measure of high-calorie consumption must be greater than low-calorie consumption after the conditioning phase (conditioning) or equal to low-calorie consumption after the test phase (extinction).

Although the amount of time spent eating, sniffing or transporting the high- and low- calorie mash during the first 5 min of observation may not agree with the measures of mash consumption, in nearly every case they did agree. Therefore, for all parts of Experiment 1, only the consumption measures are reported.

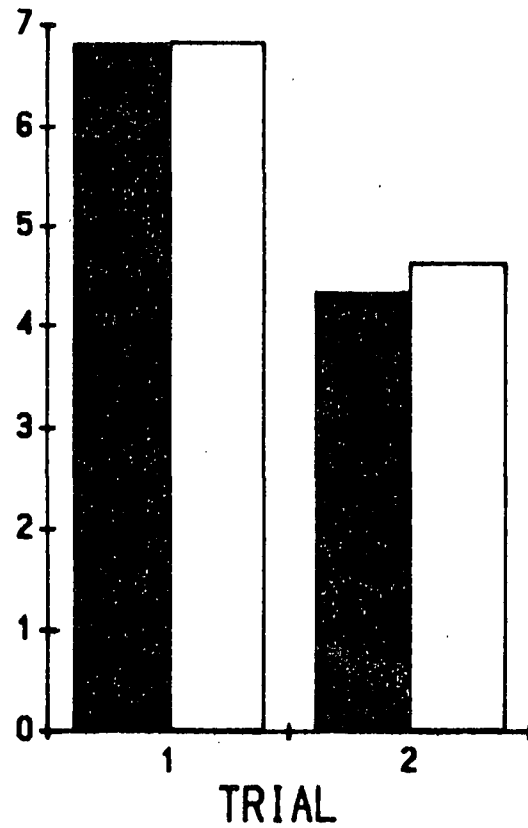
1.1.5 Results And Discussion

Figure 1 shows consumption of isocaloric diets during test trials. During this phase, hamsters did not consume more of the mash whose flavor was previously associated to the high-calorie mash (\bar{M} = 5.58 g, 16.79 g) than the mash whose flavor was previously associated to the low-calorie mash (\bar{M} = 5.73 g, 18.58 g) after 1 hr [$F(1,15) = 0.0656$, $p = .7889$] nor after 24 hr [$F(1,15) = 1.7683$, $p = .2013$]. After 1 hr, hamsters ate an equal amount of isocaloric flavored mash. After 24 hr, hamsters actually ate a greater amount of mash whose flavor was previously associated to the low-calorie mash. Thus, hamsters did not demonstrate the flavor-calorie conditioning effect.

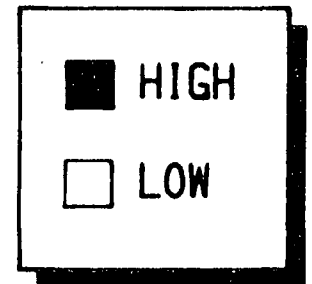
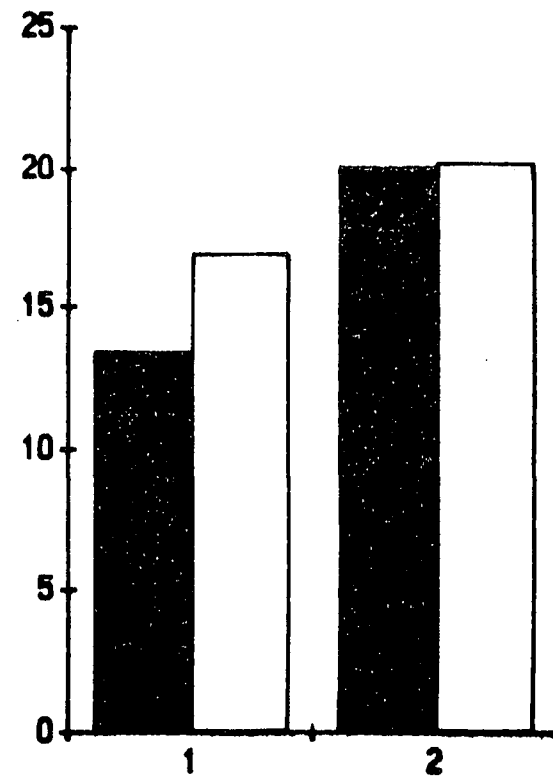
When consumption was measured after 1 hr, hamsters had consumed more mash during the first test trial (\bar{M} = 6.83 g) than the second test trial (\bar{M} = 4.48 g) [$F(1,15) = 19.0452$, $p = .0008$]. When consumption was measured after 24 hr, hamsters

Figure 1 - Mean consumption of isocaloric mash whose flavors were previously paired with a high- or low-calorie mash by hamsters after 1 hr and 24 hr.

1 HOUR



24 HOUR



consumed more mash during the second test trial ($\bar{M} = 20.10$ g) than the first test trial ($\bar{M} = 15.18$ g). [$F(1,15) = 48.8433$, $p = .0000$]. Hamsters' consumption of mash across trials appears to switch from immediate feeding to delayed feeding. Recall that until the test phase, hamsters had been presented with one mash per conditioning trial or 30 g of mash per day. Perhaps, the availability of twice as much mash (60 g) altered their feeding strategy. When presented with a small amount of food, hamsters may eat larger but fewer meals per day. When presented with a large amount of food, hamsters may prefer to eat smaller but more meals per day.

The amount of isocaloric mash hamsters consumed was independent of the trial number when measured after 1 hr [$F(1,15) = 0.0314$, $p = 0.8380$] and 24 hr [$F(1,15) = 2.7200$, $p = .1168$] (Figure 1). The hamsters appear to eat an equal amount of isocaloric mash after 1 hr and 24 hr in both trials.

Hamsters showed no preference towards visiting either flavored isocaloric mash first. Choice of each flavored mash was equally likely. Those hamsters with a high-calorie raspberry - flavor association chose raspberry mash 9 times in 16 trials (56%). Those hamsters with a high-calorie strawberry - flavor association chose strawberry mash 7 times in 16 trials (44%).

2. PART 2

In Part 1, the hamsters did not show a significant flavor-calorie conditioning effect. This outcome differs from that reported by Bolles et al. (1981) for rats. One reason for this discrepancy may be that Bolles et al.'s original procedure was

not followed exactly. Because in pilot studies we found that hamsters stored food mash in their cheekpouches, a single mash had to be presented on alternate days in order to prevent cheekpouching. Since the original mashes were different colors, when cheekpouched a ball of mash consisting of more than one color could be discovered in the hamsters' food cache. If hamsters cheekpouch and sample both diet mixes, then the mash no longer can be identified by one flavor - calorie association. Simultaneous sampling of mash during the conditioning phase results in a mixture that resembles the isocalorie mixture presented in the test phase. However, Bolles et al.'s procedure involved simultaneous presentation of the low- and high-calorie mash. Consequently in Part 2, vanilla and chocolate Sustacal (a milky liquid substance) was substituted for the flavored mash because cheekpouching of a liquid substance is unlikely. With this modification, we were able to present low- and high-calorie diets simultaneously.

2.1 Method

2.1.1 Subjects

The same subjects that served in Part 1 were used.

2.1.2 Materials

During the conditioning and test phase, a subject was given access in its homecage to two 50 ml tubes of Sustacal (a milky liquid substance manufactured by Mead Johnson which is used as a dietary supplement).

The high-calorie Sustacal liquid consisted of 145 ml of

Sustacal to 290 ml of water. This mixture was 3.4 calories per ml. The low-calorie Sustacal liquid consisted of 90 ml of Sustacal to 300 ml of water. This mixture was 2.3 calories per ml. Sustacal is manufactured in both vanilla and chocolate flavors. Therefore, no additional extract was needed in order to flavor each diet.

2.1.3 Procedure

During the conditioning phase, the subjects had ad lib access to water and 1-hr access to both Sustacal liquid diets. Placement of the tubes on the left or right side of the homecage was randomized. For eight subjects (four female, four male) vanilla Sustacal was the high-calorie diet and chocolate the low-calorie diet. The flavors were reversed for the other eight subjects. Consumption was measured once, at the end of a 1-hr period. (Sustacal liquid must be refrigerated. Thus, consumption measures past 1 hr would be confounded by spoilage effects.) Subjects were given one pellet (approximately 5g) of laboratory chow following liquid presentation. After 2 days of conditioning, a 24-hr deprivation period when no food or Sustacal liquid was available was implemented. This cycle was repeated four times prior to the test phase.

On test days, the subjects were offered both tubes, but at this time the liquid in both tubes were of equal caloric density, consisting of an equal mixture of both diets. The only difference between the two tubes was the flavors that had previously been correlated with caloric density. Consumption was measured at the end of a 1-hr period. Subjects were given

one pellet (approximately 5g) of laboratory chow following liquid presentation.

Five consecutive test days were implemented before four subjects, two from each group (one male, one female) were randomly chosen to serve in a further test. This group of four subjects received 5 more days of testing with the original high- and low-calorie diets but with the vanilla and chocolate flavors reversed. The flavors-reversed group was added to test the tenacity of the conditioned flavor preferences when the unconditioned stimulus conditions were reversed. That is, to compare the strength of the conditioned stimulus to the unconditioned stimulus.

2.1.4 Statistics

Data from the conditioning and test phases are analyzed with the same experimental design outlined in the statistics section of Part 1 (Sec. 1.1.4).

Data from the flavors-reversed group were also analyzed with the same experimental design, a within group design with two fixed factors, trial and caloric density (high or low). A switch to the high-calorie liquid, which now has the opposite flavor than it had originally, is evidenced by a higher consumption measure for the high-calorie liquid.

2.1.5 Results And Discussion

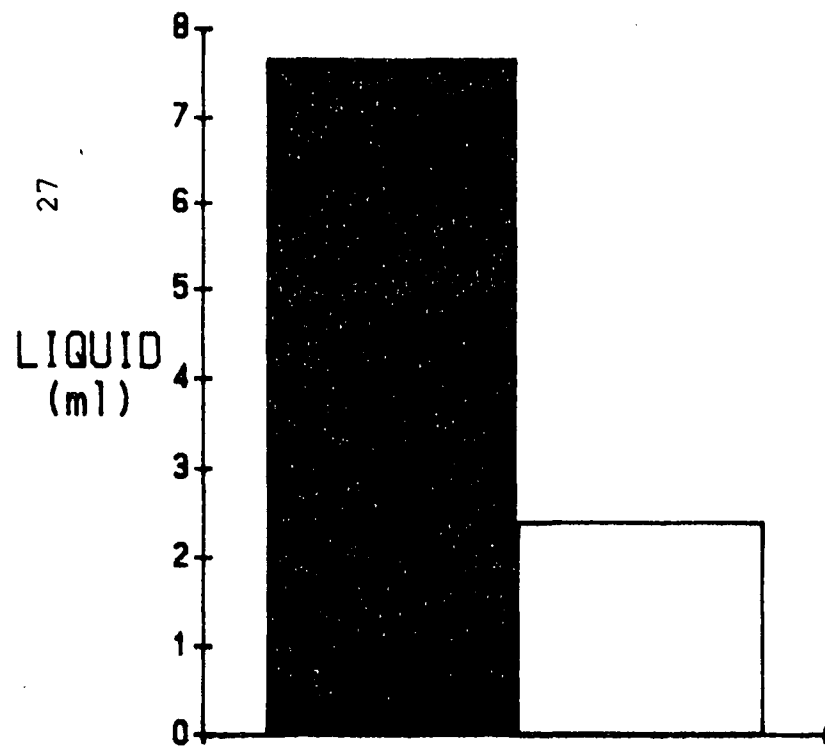
As shown in Figure 2, hamsters consumed more high calorie liquid during the conditioning phase [$F(1,15)=42.6651$, $p=.0001$]. In the test phase, hamsters also consumed more of the isocaloric liquid whose flavor was previously paired with a high-calorie liquid [$F(1,15)=22.0693$, $p=.0005$] (Figure 2). Although hamsters were willing to sample from both isocaloric diet mixes, they did consume more high-calorie liquid. Thus, they did demonstrate the flavor-calorie conditioning effect.

As shown in Figure 3, over test trials consumption of the isocaloric liquids whose flavors were previously paired to high- or low-calorie Sustacal converged. This increase in consumption of the isocaloric liquid whose flavor was previously paired to the low-calorie liquid coupled with the decrease in the consumption of the liquid whose flavor was previously paired to the high-calorie liquid represents extinction [trial x flavor interaction; $F(4,60)=5.5475$, $p=.0010$]. Thus, within 5 trials of isocaloric presentation hamsters no longer preferred the flavor which previously represented a high-calorie food. The flavor-calorie conditioning effect appears to be easily extinguished in hamsters.

When hamsters were given 5 additional days with the flavors reversed, there was a marginal difference in the amount of liquid consumed [$F(1,3)=8.4440$, $p=.0639$]. Hamsters consumed an average of 7.45 ml of the liquid whose flavor was originally paired with high-calorie Sustacal, but is now paired with low-calorie Sustacal and an average of 6.78 ml of the liquid whose

Figure 2 - Mean consumption of high- and low-calorie Sustacal liquid by hamsters during the conditioning and test phases.

CONDITIONING



TEST

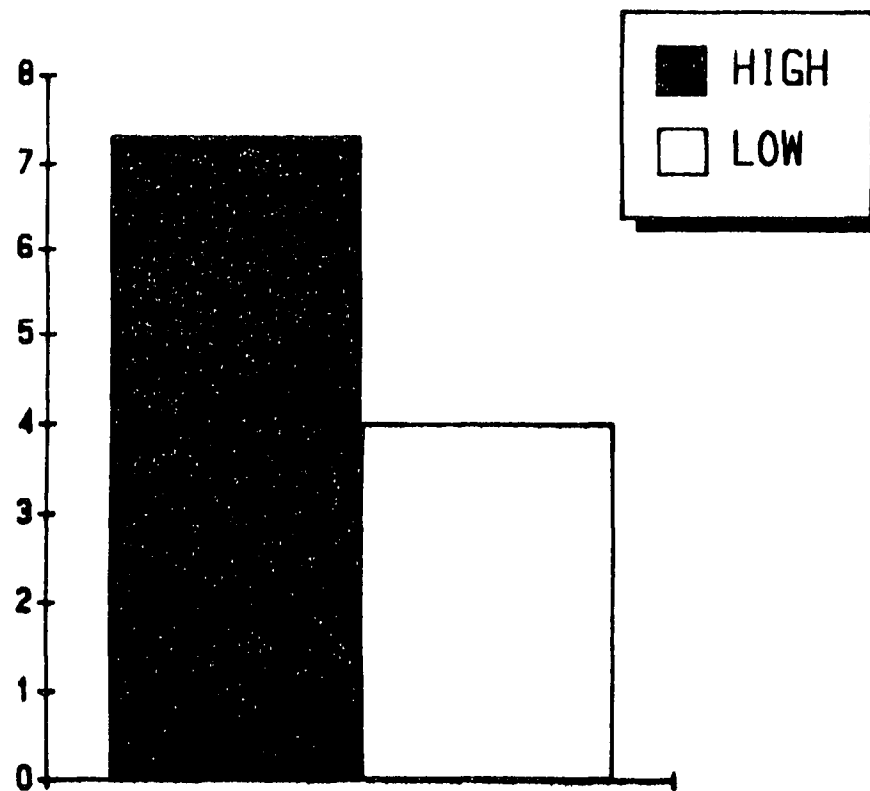


Figure 3 - Mean consumption of isocaloric liquid associated with a flavor previously paired to high- or low-calorie Sustacal by hamsters in the test phase.

TEST

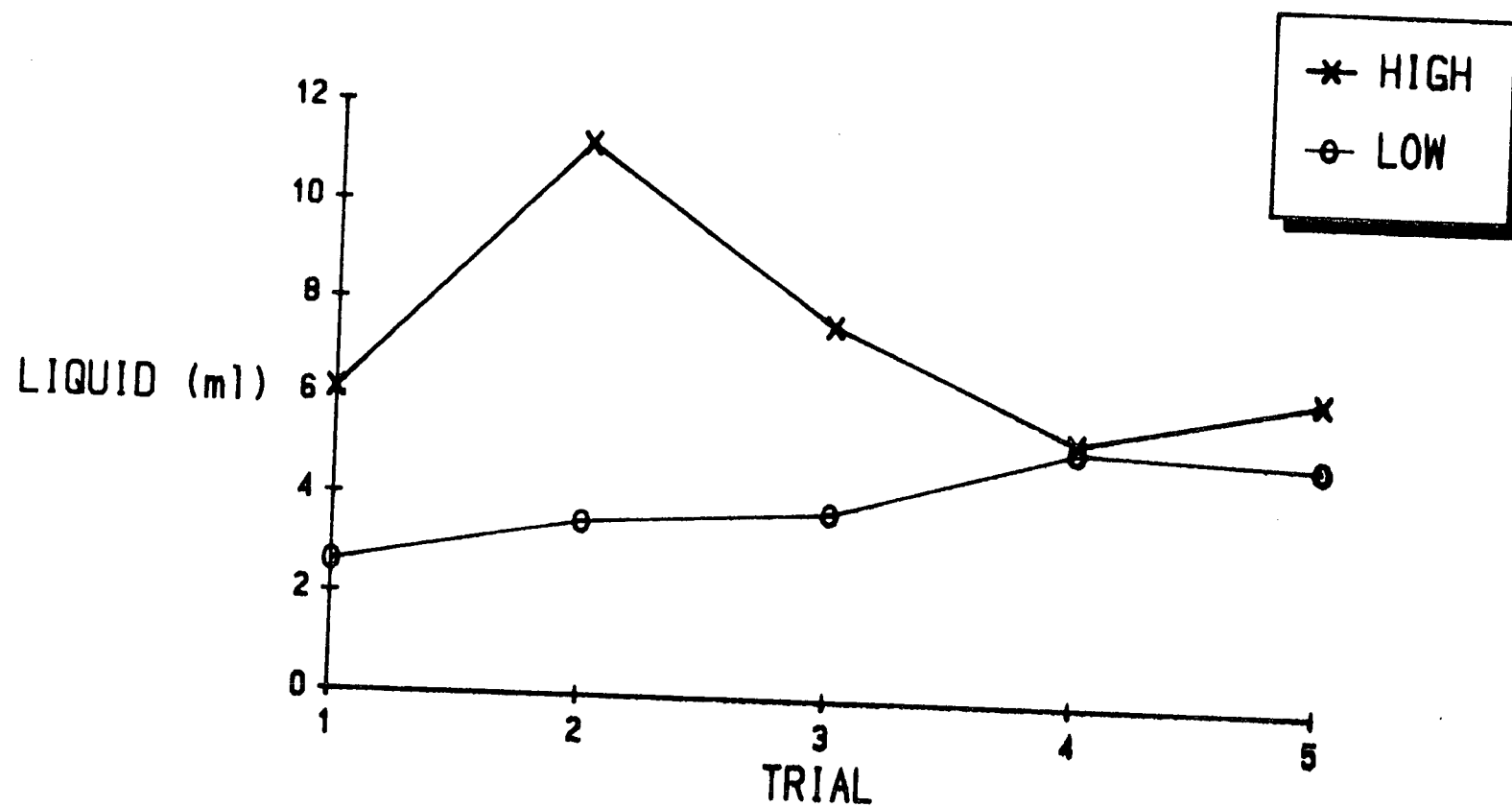
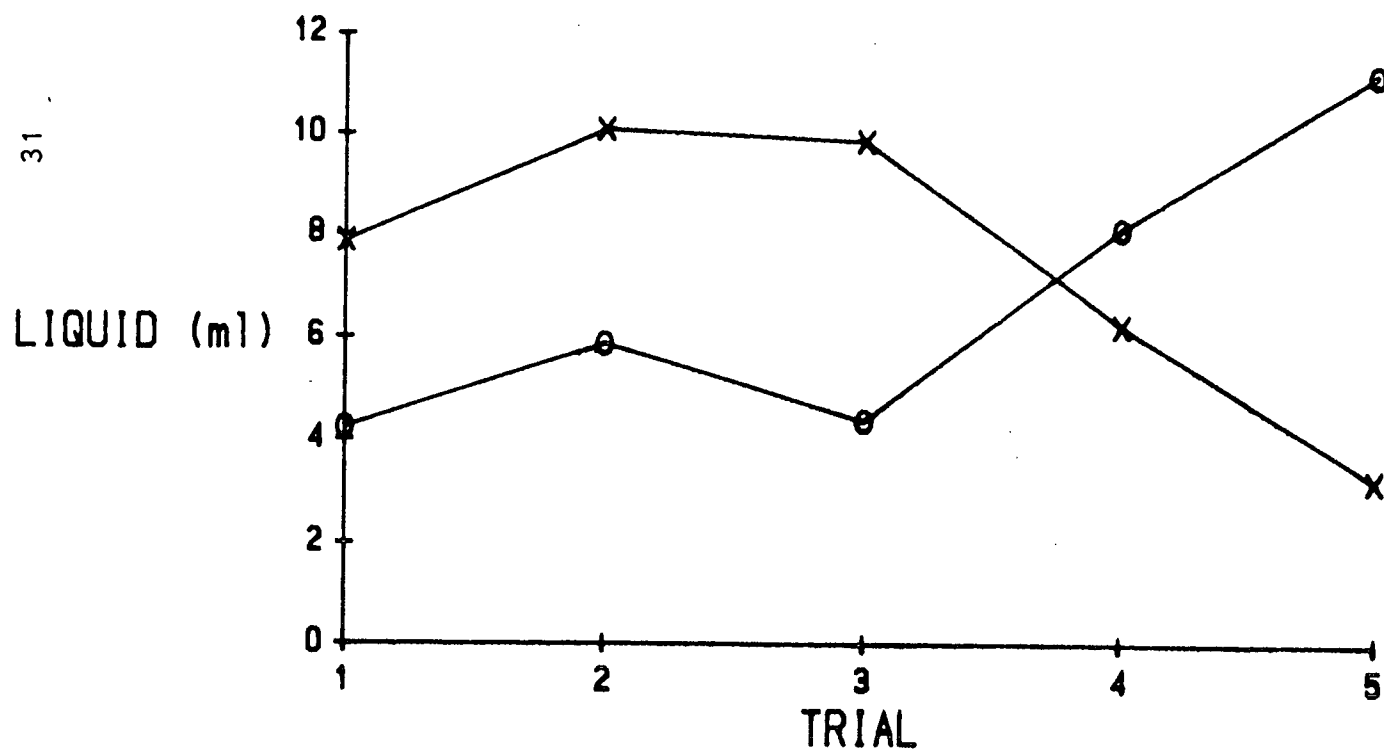


Figure 4 - Mean consumption of original high- and low-calorie flavor associated Sustacal liquid by hamsters given additional trials with the flavors reversed.

FLAVORS REVERSED



x HIGH
o LOW

flavor was originally paired with low-calorie Sustacal, but is now paired with high-calorie Sustacal.

Although overall consumption measures indicate that hamsters continued to prefer the original high-calorie - flavor association, the marginally significant [$F(4,12)=2.8001$, $p=.0742$] interaction between trial and caloric density depicts an increase in consumption of the original low-calorie - flavor liquid pair (i.e., high-calorie liquid) and a decrease in the consumption of original high-calorie - flavor liquid pair (i.e., low-calorie liquid) (Figure 4). In Figure 4, the high-calorie measure refers to the isocaloric liquid whose flavor was previously paired to a high-calorie diet but is now, upon presentation, paired to a low-calorie diet; and vice versa for the low-calorie measure. Thus, a switch in preference appears to have begun. Therefore, hamsters will decrease their preference for a food when the flavor associated with that food no longer represents a higher quality food. As well, hamsters will adopt a preference for a food whose flavor has recently been paired with an enriched food.

3. PART 3

In Part 1 hamsters exposed to a successive discrimination procedure did not demonstrate the flavor-calorie conditioning effect. In Part 2 hamsters exposed to a simultaneous discrimination procedure did demonstrate the flavor-calorie conditioning effect, but the effect was less robust than that discovered by Bolles et al. (1981) when rats served as subjects. As opposed to rats, hamsters were more willing to eat

or drink both available mashes or liquids. Because of this apparent species difference, a study of flavor-calorie association in another species was warranted. Thus, in Part 3 flavored mash was presented to Mongolian gerbils in the same fashion as Part 1.

3.1 Method

3.1.1 Subjects

Sixteen experimentally naive Mongolian gerbils (Meriones unguiculatus) (eight female, eight male) were housed individually in opaque-sided cages in a colony on a reversed 12-hr light/ 12-hr dark (dark cycle began at 8:00 a.m.). They had unlimited access to water.

3.1.2 Materials

The materials were identical to those used in Part 1.

3.1.3 Procedure

The procedure was identical to that used in Part 1 except that the gerbils were only offered 10g of each diet, and after completion of the 4 test days the group was randomly divided into three groups. One group received three more days of testing (extinction group), one group received three more days of testing with the original high- and low-calorie diets but with the raspberry and strawberry flavors reversed, and one group received three more days of testing with the original high- and low-calorie diets with no flavors added. The extinction group was added to test the tenacity of the conditioning effect.

Since hamsters had 5 days of isocaloric presentation and gerbils had only two, three more days of isocaloric presentation allows us to roughly compare the extinction rate (or the tenacity of the conditioning effect) between species. The flavors-reversed group was added to test the tenacity of these preferences when the unconditioned stimulus conditions were reversed. The no flavors group was added to test if properties other than taste are being used as cues for diet choice.

3.1.4 Statistics

Data from the test phase and additional test conditions are analyzed with the same experimental design outlined in the statistics section of Part 2 (Sec 2.1.4).

If gerbils continue to prefer the isocaloric mash whose flavor was previously paired with high-calorie mash, then we can conclude that the conditioning effect is robust. If gerbils choose the high-calorie mash when no flavors are added to the mash, then we can assume that other cues in addition to taste, such as texture or odor cues, may aid in detecting the high-calorie mash.

3.1.5 Results And Discussion

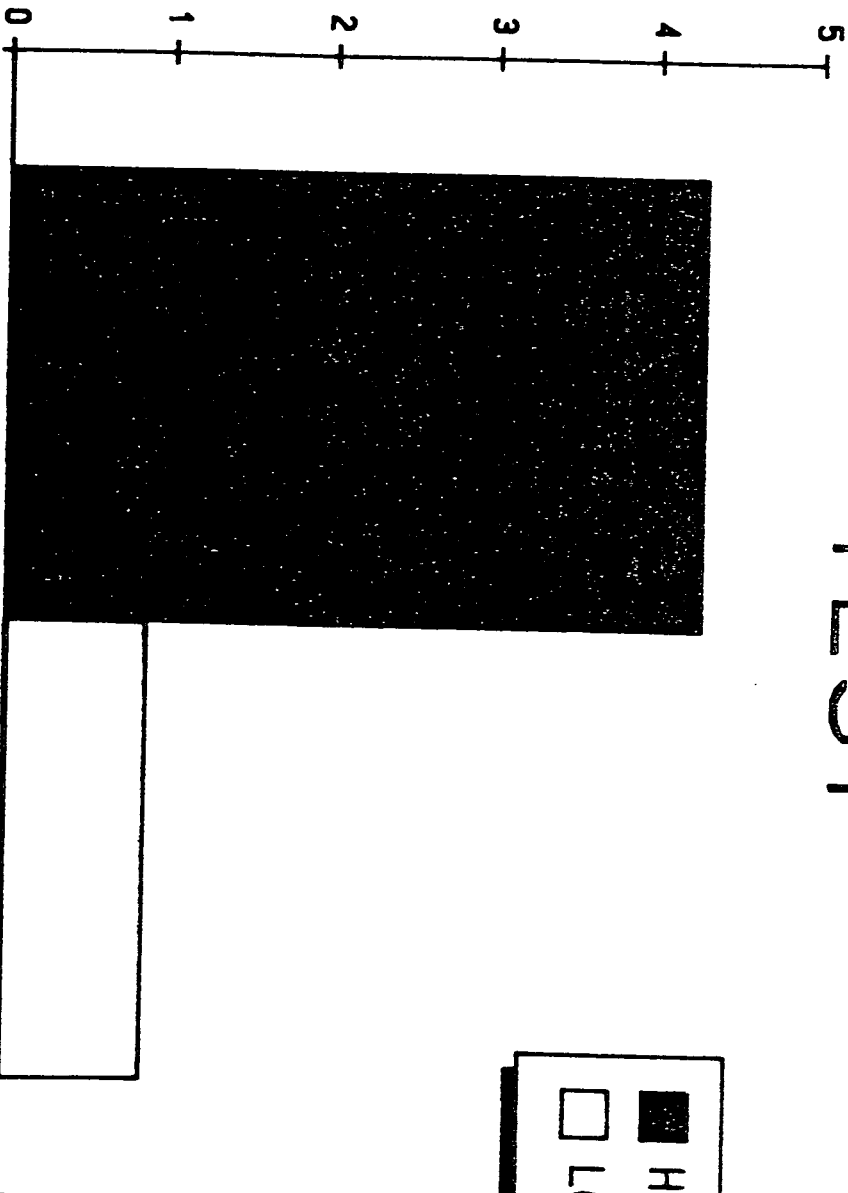
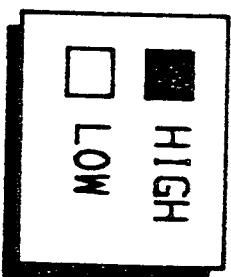
As shown in Figure 5, gerbils consumed more of the isocaloric mash whose flavor was previously associated with high-calorie mash [$F(1,15)=60.9009$, $p=.0000$]. Thus, gerbils did demonstrate the flavor-calorie conditioning effect. Unlike hamsters, this effect was robust. As compared to hamsters, gerbils were less likely to sample from the isocaloric mash

Figure 5 - Mean consumption of high- and low-calorie mash
by gerbils in the test phase.

TEST

36

MASH (g)



whose flavor was previously paired to the low-calorie mash.

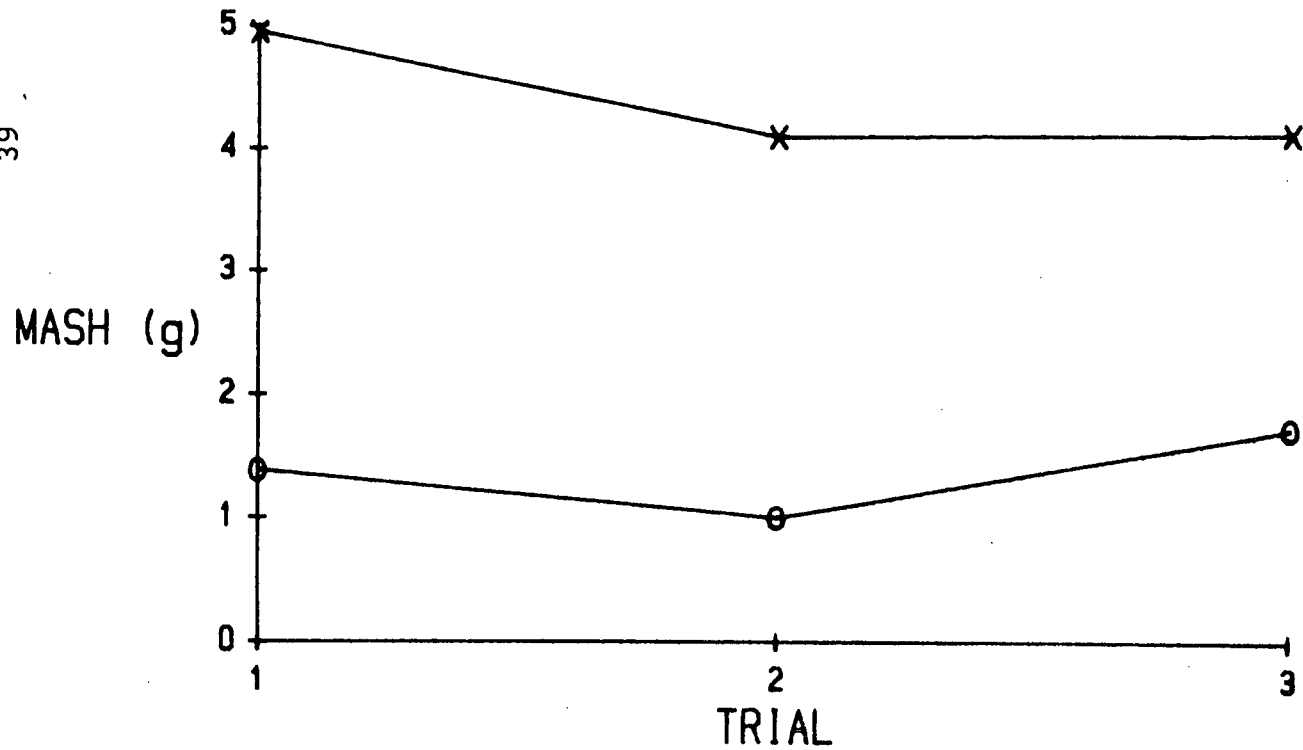
When gerbils were given extended presentation of the isocaloric mash, gerbils continued to prefer the mash whose flavor was previously associated with high-calorie mash [$F(1,3)=9.0561$, $p=.0590$]. Gerbils consumed a mean 4.39 and 1.37 g of isocaloric mash whose flavor was previously associated with high- calorie and low-calorie mash, respectively. Figure 6 illustrates the strength of the conditioning effect across trials. No interaction existed between consumption per trial and caloric density [$F(2,6)=1.2097$, $p=.3629$]. Thus, unlike hamsters, the flavor-calorie conditioning effect is not easily extinguished in gerbils.

When given 3 additional days with the flavors reversed, gerbils exclusively consumed the high-calorie mash whose flavor was originally paired with low-calorie mash. [$F(1,3)=83.2328$, $p=.0055$]. Gerbils consumed 4.57 g and 0.0 g of the high- and low-calorie mash, respectively.

Although no interaction was observed between the amount of mash consumed per trial and caloric density [$F(2,6)=2.7037$, $p=.1452$], Figure 7 illustrates the strong avoidance of low-calorie mash (i.e., the mash whose flavor was originally paired to the high-calorie mash) by gerbils. In Figure 7, the high-calorie measure refers to the isocaloric mash whose flavor was previously paired to a high-calorie mash but is now, upon presentation, paired to a low-calorie diet; and vice versa for the low-calorie measure. Thus, gerbils readily switched their mash preference in accordance with mash quality regardless of

Figure 6 - Mean consumption of isocaloric mash associated with a flavor previously paired to high- or low-calorie Sustacal by gerbils given additional isocaloric mash presentation (extinction training).

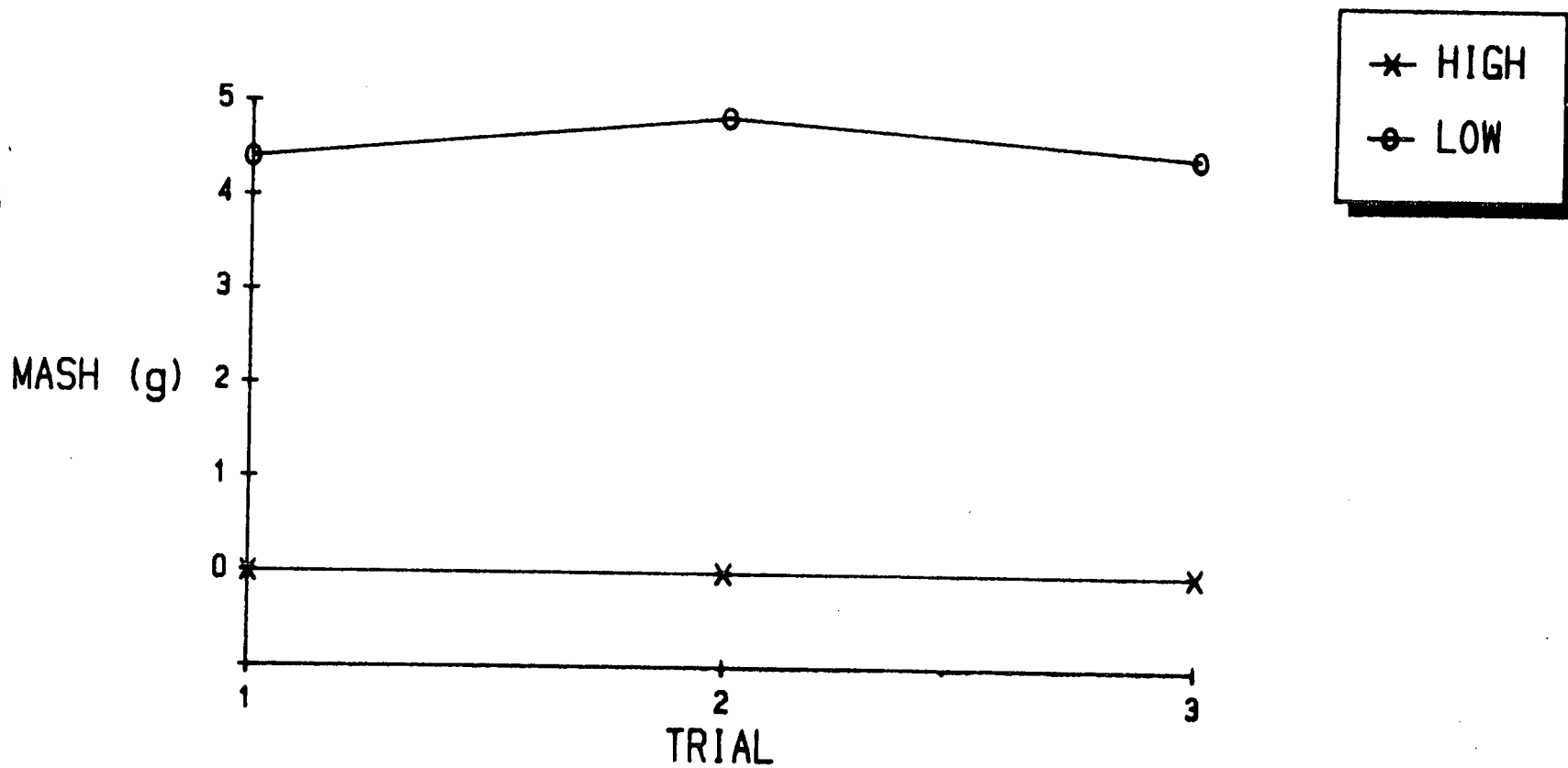
EXTINCTION



x HIGH
o LOW

Figure 7 - Mean consumption of high- and low-calorie mash whose flavors are reversed by gerbils given 3 additional days of mash presentation.

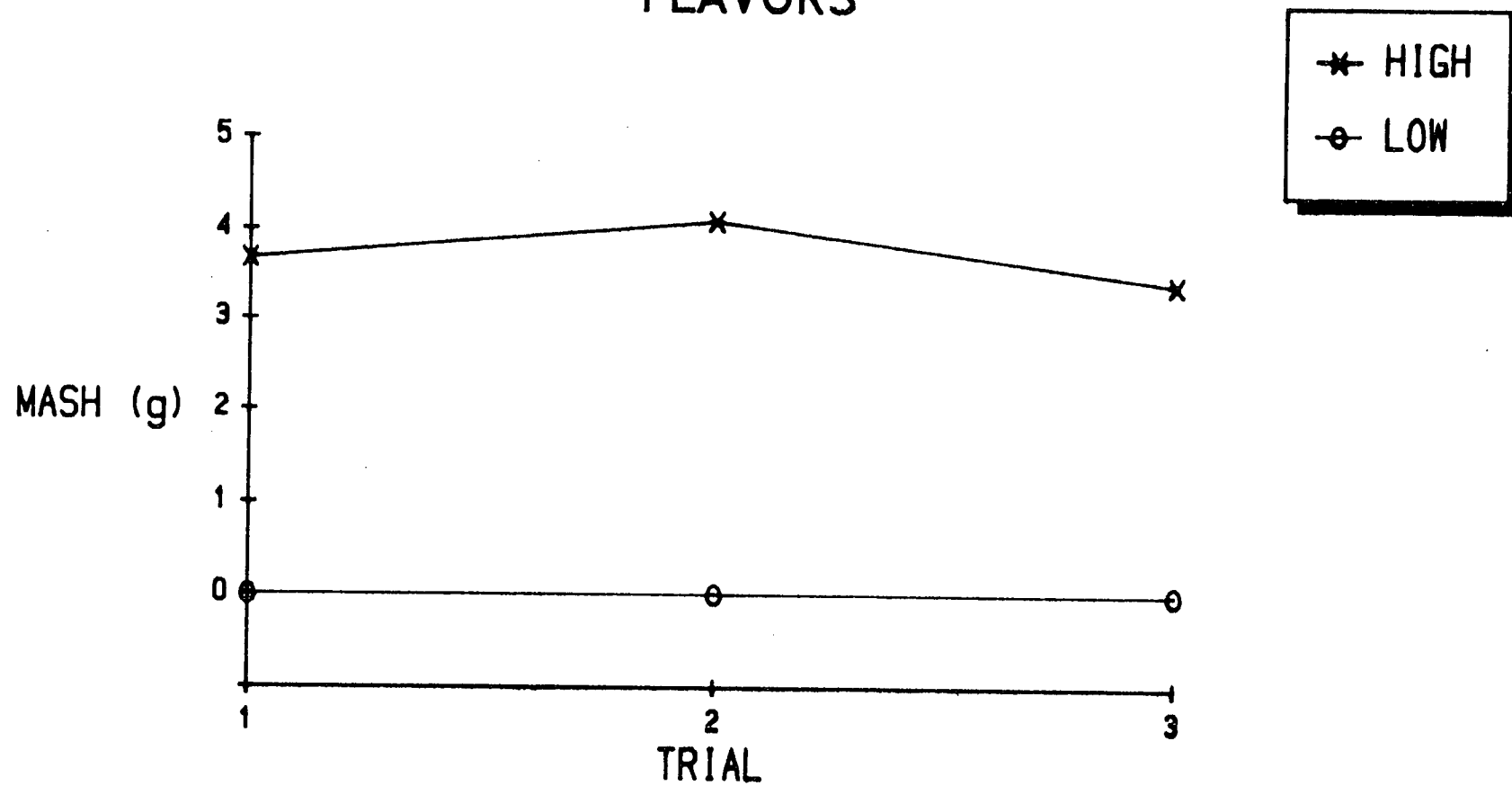
FLAVORS REVERSED



the prior association formed from flavor-calorie conditioning. Although gerbils may use the information gained from flavor-calorie conditioning when choosing between two isocaloric diets of different flavors, they do not rely exclusively on taste cues when offered foods of different caloric density.

When given 3 additional days with no flavors added to mash, gerbils exclusively consumed high-calorie mash [$F(1,3)=292.2598$, $p = .0023$]. Gerbils consumed a mean 3.72 g and 0.0 g of high- and low-calorie mash, respectively. Figure 8 illustrates the strong avoidance of low-calorie mash by gerbils. This further demonstrates the gerbils ability to use cues other than taste when choosing the high-calorie food if presented with foods of different caloric density that have the same flavor or essentially no flavor associations. In addition, the gerbils' ability to choose a high-calorie food does not appear to be affected by prior flavor associations to that particular food.

Figure 8 - Mean consumption of high- and low-calorie mash
by gerbils given 3 additional days with no flavors added to the
mash.

NO
FLAVORS

III. EXPERIMENT 2

The purpose of Experiment 2 was to analyze the food choices of the same hamsters and gerbils as in Experiment 1 in a foraging situation where travel is necessary. Travel is an additional cost of foraging that may affect diet selection. We were interested in detecting a change in preference for a known high-calorie food source that a subject must now actively seek. Subjects were allowed to forage on an 8-arm radial maze on which one-half of the arms were baited with high-calorie Sustacal and one-half with low-calorie Sustacal. Each subject was allowed to visit and/or drink from eight arms. We were interested in seeing if subjects would prefer to visit and drink from those arms which contained the high-calorie Sustacal. If flavor-calorie associations are an important factor in foraging in natural settings, than we would expect subjects to readily learn to visit places containing the high-calorie food.

4.1 Method

4.1.1 Subjects

The same hamsters and gerbils that served as subjects in Experiment 1 served in Experiment 2.

4.1.2 Materials

During testing, subjects were transported in their homecage from the housing room into the testing room. An 8-arm radial maze was elevated (60cm) in the center of a 3.2m x 2.8m x 2.8m testing room. The dimensions of each arm were 30cm x 15.5cm and

the diameter of the center platform was 90cm. Each arm was flat and without walls. A small receptacle for food or liquid was located at the distal end of each arm.

Extramaze visual cues consisted of the following: two swivel chairs, a garbage can, a large wooden board (3.0m x 2.5m), six shelf doors, a countertop, and a door. No intramaze cues were provided. The experimenter sat in the same swivel chair in the same corner of the testing room for each trial.

The high- and low-calorie Sustacal was the same as in Experiment 1.

4.1.3 Procedure

Hamsters were first reconditioned to their original flavor-calorie associations. Gerbils were conditioned to a new flavor-calorie association that used Sustacal liquid as a diet mix rather than mash. Both species were presented with Sustacal liquid in the same fashion as outlined in Experiment 1, Part 2.

Prior to the testing phase, each subject was allowed to explore the unbaited maze for 5 consecutive days, 10 min each day. During subsequent test phases, Sustacal liquid (1ml) was located in the receptacle at the end of each maze arm.

For each subject, one-half of the arms contained high-calorie Sustacal and one-half contained low-calorie Sustacal. For each subject, high- and low-calorie Sustacal flavor associations remained the same as in Experiment 1. The assignment of each arm location - Sustacal-flavor association was random for each subject and remained the same for each trial. However, hamsters and gerbils were randomly paired such

that a hamster foraging on a maze where arms #2, #4, #6, and #7 are high-calorie vanilla Sustacal is matched to a gerbil foraging under the same conditions.

After being placed in the center of the maze, subjects were allowed to visit a total of eight arms and drink the Sustacal liquid. Revisiting an arm was also considered as a visit. Accordingly, a subject could visit eight arms without entering all available arms. Arm choice or a visit was made when the subject's hind paws transversed the arm entrance. A drink was taken when the subject's tongue entered the receptacle at least once. Many subjects sampled by taking a single lick of Sustacal. This was considered as drinking in this context. Not drinking, then, is evident by the subject's failure to taste the liquid.

After eight choices were made the subjects were removed from the maze apparatus, and returned to the housing room.

4.1.4 Statistics

Data for both hamsters and gerbils were analyzed using the same statistics.

A within-group analysis of variance with two fixed factors, trial and caloric density (high and low), was used when analyzing reconditioning measures from hamsters and conditioning measures from gerbils.

When the subjects visited each arm on the maze, arm location (number) and whether or not the subject drank from the arm was noted. The number of visits to the high-calorie arm locations were tallied and divided by the total number of

possible visits per trial. If considering the subjects' performance after four choices, then the total number of visits is four. Thus, a subject who visited one high-calorie arm location has visited 25% of the possible high-calorie arm locations. To determine drinking performance subjects received one point for either drinking from a high-calorie arm location or not drinking from a low-calorie arm location. This method of scoring was necessary to control for subjects who drank from all arms or no arms. These points were tallied and divided by the total number of possible visits per trial. Subjects received a total score for the number of visits to and drinks from high-calorie arm locations. These scores were compared to chance level (50%) using a t-test statistic.

Preference ratings were also obtained for each subject. Since subjects could visit eight arms, a score of eight identified the subjects first choice, a highly preferred arm location. The subjects' second choice received a score of seven; the third choice received a score of six; fourth choice is five; and so on. Arms that were revisited or not visited received a score of zero. For each trial a preference rating score for each arm was obtained for each subject. The preference scores were summed across trials. Preference ratings allows us to depict a consistent preference for one or more arms, response patterning or circling, or a memory-based strategy.

An arm that is preferred will have a high preference score. A circling strategy will be evident if the subject begins each

trial in the same location and circles in the same direction. If so, the graph illustrating preference score and arm location will have a peak marking the arm that begins the circuit and a progressively lower preference rating for each arm location following the peak. If the graph has no peaks and the subject has a high performance score, then the lack of response patterning may indicate that the subject used a memory-based strategy or that the subject began each trial in a different arm location.

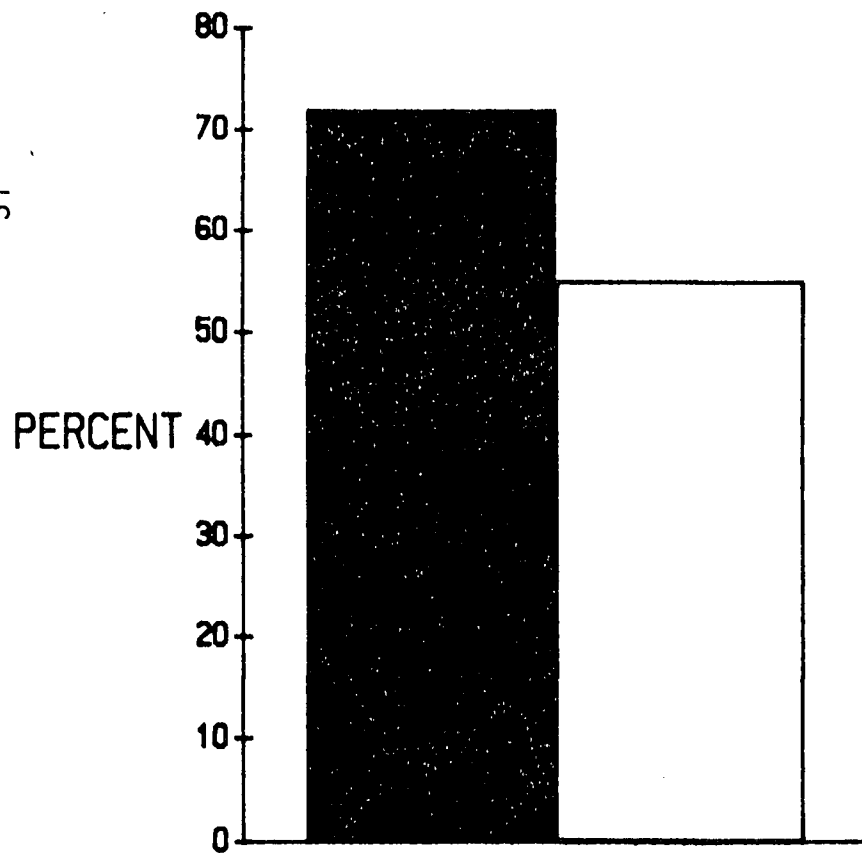
4.1.5 Results And Discussion

For Experiment 2, eight hamsters were reconditioned to their original caloric density - Sustacal-flavor association. After 5 conditioning days, hamsters consumed more high-calorie liquid ($\bar{M} = 7.39$ ml) than low-calorie liquid ($\bar{M} = 2.49$ ml) [$F(1,7) = 23.3512$, $p = .0023$].

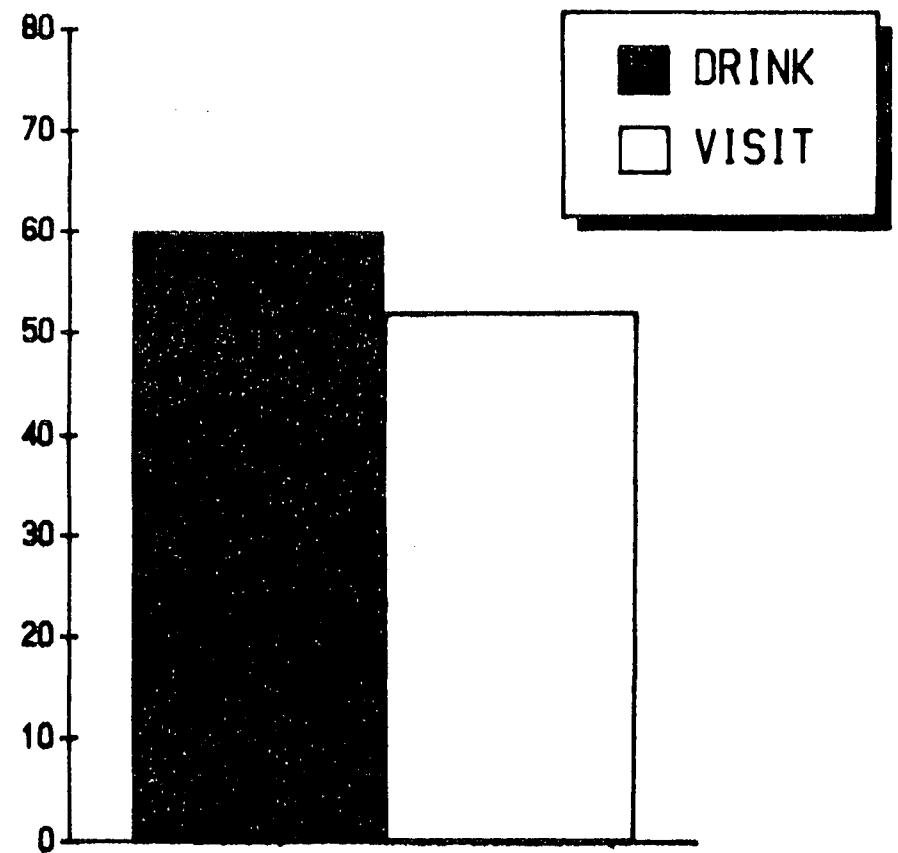
On the 8-arm radial maze where one-half of the arms were baited with high-calorie Sustacal and one-half with low-calorie Sustacal, of the first four choices, 54% of the visits were to high-calorie arm locations. This was not above chance (50%) [$t(7) = .95$, $p = .3800$]. Of the first four choices, 66% of the drinks were taken at high-calorie arm locations. This was above chance [$t(7) = 3.8$, $p = .0089$]. As shown in Figure 9, for all eight choices, 55% of the visits were to high-calorie arm locations. This was not above chance [$t(7) = 2.12$, $p = .0780$]. For all eight choices, 72% of the drinks were taken at high-calorie arm locations (Figure 9). This was above chance [$t(7) = 7.72$, $p = .0002$]. Thus, hamsters did not prefer to visit the

Figure 9 - The percentage of visits to and drinks from arm locations that contain high-calorie Sustacal liquid for both hamsters and gerbils.

HAMSTERS



GERBILS



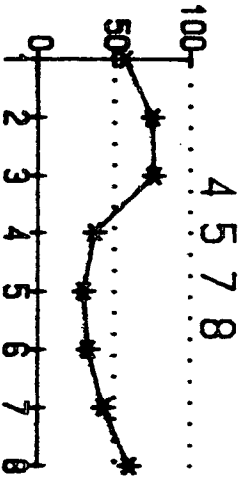
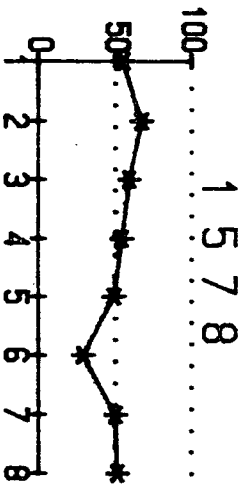
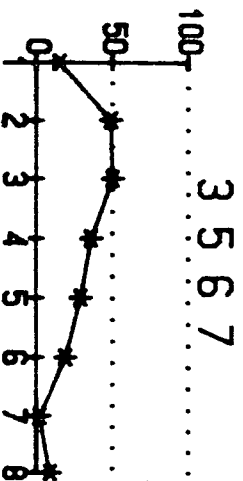
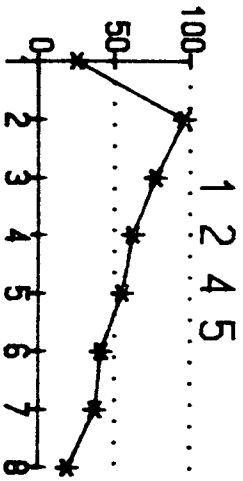
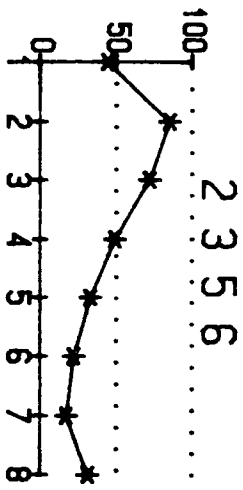
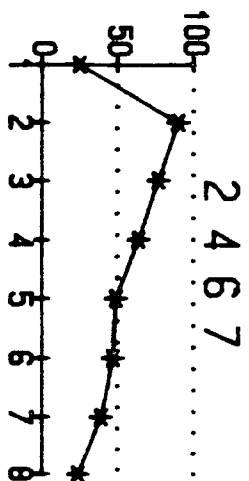
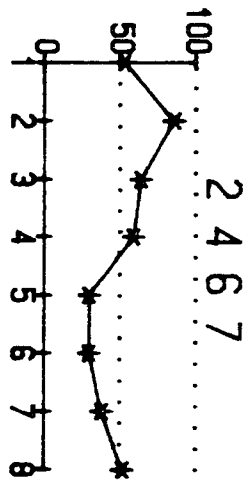
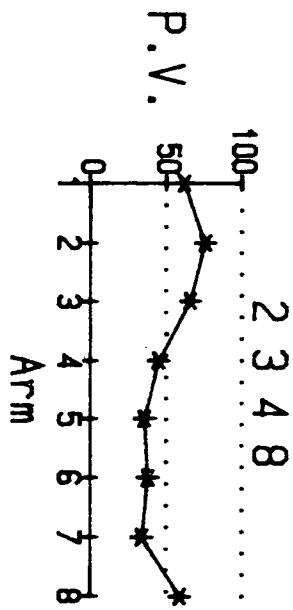
high-calorie arm locations. However, they did prefer to drink from these locations.

Figure 10 depicts the arm preference rating for each hamster. Arm preference is calculated by summing the preference rating for each arm across trials (refer to the statistics Sec. 4.1.4. for further details). Although each hamster was randomly assigned different high-calorie arm locations, they began each trial at the same arm (viz. arm #2), and circled the maze in the same direction for each trial. In Figure 10, the high-calorie arm locations are given for each subject. Each arm preference graph shows that the subject did not selectively visit the high-calorie arm locations. However, if these subjects were circling the maze in order to locate high-calorie arms, then the observed 55% of visits to high-calorie arms is not surprising since 50% of the arms contained high-calorie Sustacal. Their decision of whether or not to drink from an arm location provides more information about their diet preferences. Their foraging strategy, mainly using an algorithm, dictates their arm location preferences. That is, the arm which is most preferred is that arm which is next to the arm currently visited.

For Experiment 2, eight gerbils were conditioned to prefer high-calorie Sustacal liquid using taste cues. They consumed more high-calorie liquid ($\bar{M} = 6.18$ ml) than low-calorie liquid ($\bar{M} = 0.58$ ml) [$F(1,7) = 111.5731$, $p = .0001$].

When foraging on the 8-arm radial maze under the same conditions as the hamsters, of the first four choices, 49% of

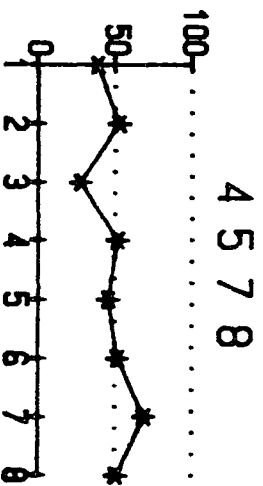
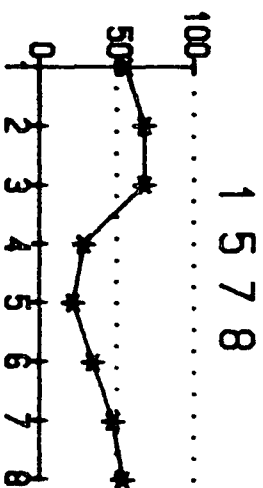
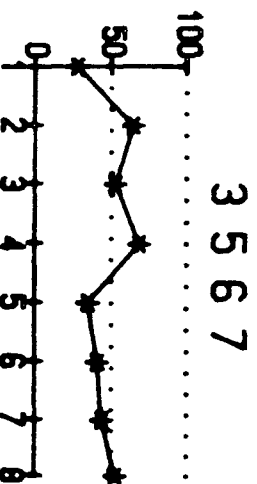
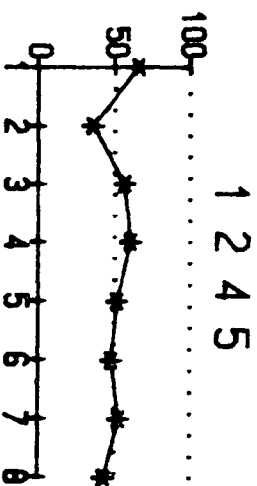
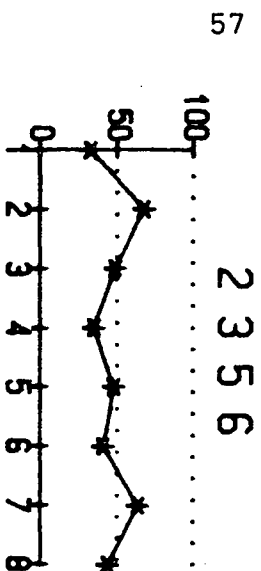
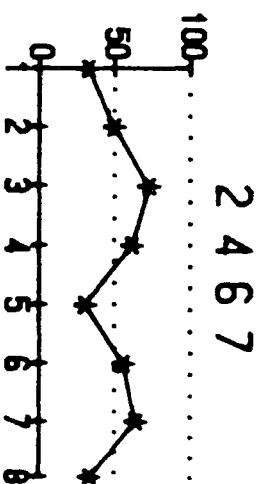
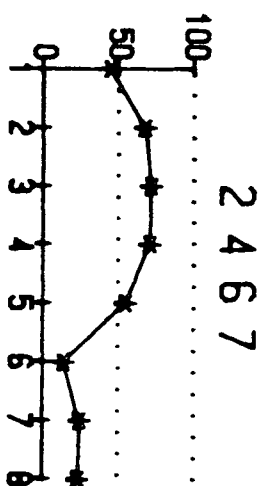
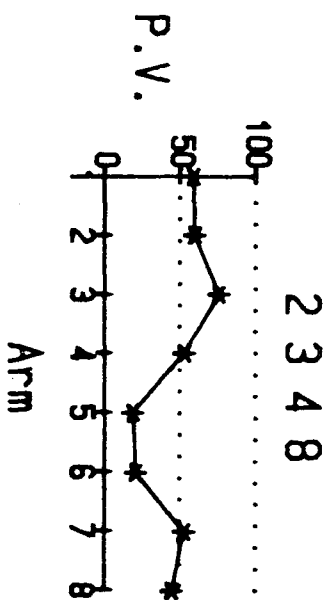
Figure 10 - The arm preference totals, preference value, summed across trials for each hamster visiting high- and low-calorie arm locations on the 8-arm radial maze. The arms containing high-calorie Sustacal liquid are noted for each subject.



the visits were to high-calorie arm locations. This was not above chance (50%) [$t(7) = .20$, $p = .8500$]. Of the first four choices, 56% of the drinks were taken at high-calorie arm locations. This was not above chance [$t(7) = .87$, $p = .4100$]. As shown in Figure 9, for all eight choices, 52% of the visits were to high-calorie arm locations. This was not above chance [$t(7) = 1.02$, $p = .3400$]. For all eight choices, 60% of the drinks were taken at high-calorie arm locations (Figure 9). This was not above chance [$t(7) = 1.55$, $p = .1600$]. Gerbils, like hamsters, did not prefer to visit the high-calorie arm locations. However, unlike hamsters, gerbils did not prefer to drink from high-calorie arm locations.

Figure 11 depicts the arm preference rating for each gerbil. According to Figure 11, no arm was preferred across all trials, and no overall circling strategy is visible. Thus, unlike hamsters, gerbils did not adopt a foraging strategy in order to either locate or consume food rewards.

Figure 11 - The arm preference totals, preference value, summed across trials for each gerbil visiting high- and low-calorie arm locations on the 8-arm radial maze. The arms containing high-calorie Sustacal liquid are noted for each subject.



IV. EXPERIMENT 3

The purpose of Experiment 3 was to compare the hamsters' performance in a radial-arm maze on which the arms were equally baited to both their performance in an unequally baited radial-arm maze as well as to other species' performance in an equally baited radial-arm maze. Hamsters were placed on a 17-arm radial maze baited with single sunflower seeds. In the first phase, the foraging strategy utilized in collecting these seeds was noted. In the second phase, four of the baited arms were blocked. After the hamsters made 13 choices, they were temporarily removed from the maze, while the blocks were withdrawn. The hamsters' subsequent four choices when returned to the maze were recorded. This test allowed the hamsters to demonstrate a memory-based strategy for collecting seeds in a maze situation.

5.1 Method

5.1.1 Subjects

Five experimentally naive Golden hamsters (two female, three male) were housed individually in opaque-sided cages in a colony on a reversed 12-hour light/ 12-hour dark cycle (dark cycle began at 8:00am). They had unlimited access to water and were maintained at 80% of their free-feeding body weight. They were tested during the last third of the dark cycle.

5.1.2 Materials

A 17-arm radial maze was centrally positioned on the floor in a 3.2m x 2.8m x 2.8m room. The dimensions of each arm were 60cm x 13cm x 14cm and the diameter of the center platform was 72cm. The top of each arm was covered by translucent plastic. The entire maze was painted gray.

Extramaze visual cues consisted of the following: three large posters (90cm x 60cm) and six small pictures (15cm x 15cm) attached to the walls about 1.5m above the floor, scattered boxes, a garbage can, two chairs, a door, six shelf doors, and a countertop. No intramaze cues were provided. Sunflower seeds were strewn around the outside of the maze to prevent the subjects from using food odors as cues as to whether or not a particular arm was baited.

5.1.3 Procedure

Prior to the testing phases, each hamster was allowed to explore the unbaited maze for 7 consecutive days for approximately 30 min each day. During subsequent test phases, a single sunflower seed was located in a small receptacle at the end of each maze arm. During Phase 1 (Day 1 to Day 14), each hamster was allowed access to the maze for 10 min or until 17 arms were visited. All arm choices were recorded. An entry into an arm was defined as placement of all four paws within the arm - with or without seed removal. During Phase 2 (Day 15 to Day 25), the entrance to four randomly selected arms was blocked with wire mesh. After 13 arm choices, the hamster was placed

within its homecage, the blocks were removed, and the hamster was returned to the maze. The interval between removal and replacement of the subject was approximately 10 s. The first four choices after replacement were recorded.

The purpose of Phase 2 was to investigate the hamsters' use of a memory-based strategy for foraging. If a response strategy was being used to collect the sunflower seeds, blocking a certain number of arms would limit the efficiency of this strategy. Hamsters who successfully visited the previously blocked and still baited arms necessarily rely on a memory-based foraging strategy.

During Phase 1, the homecage was placed in the center of the maze. An inverted V-shape wire mesh ladder (15cm wide) that allowed the hamster to leave and reenter the cage was randomly placed in one of the four sides of the cage. Access to the homecage was provided so that the hamsters' could transport seeds back to its cache. Since this behavior was not observed, during Phase 2, only the ladder was placed in the center of the maze. Each hamster was placed on the top of the ladder at the beginning of each test session and when being returned to the maze in Phase 2.

5.1.4 Statistics

Analysis of the hamsters' performance on the 17-arm equally-baited radial maze involves accuracy scores, preference ratings, and patterning measures.

Two types of accuracy scores are generated. The first accuracy score is the number of correct visits (i.e., visiting

baited arms) averaged across all subjects and reported for each trial. This is accuracy across trials. The second accuracy score is the number of correct visits averaged across trials reported for each arm choice. This is accuracy within trials.

Preference ratings were obtained in the same fashion as outlined in Experiment 2 (Sec. 2.1.4). However, the highest preference score is 17 since the maze consisted of 17 arm locations.

To look for possible response strategies the number of choices as a function of the chosen arms position relative to the last choice was calculated. Choosing the arm directly to the left or right of the arm currently visited is + or -1; choosing the arm two doors to the left or right of the arm currently visited is + or -2; three doors is + or -3; and so on.

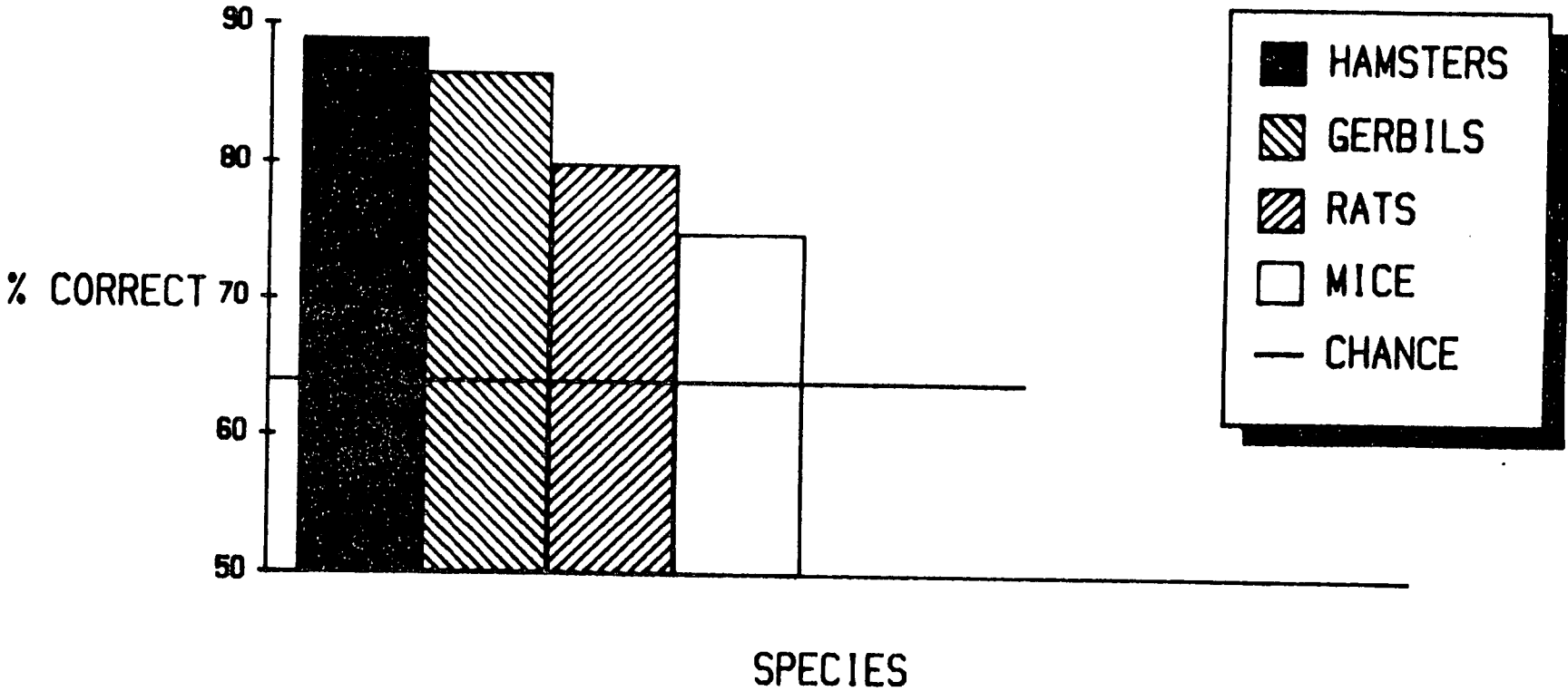
5.1.5 Results And Discussion

Each hamster quickly learned to locate the sunflower seeds at the end of each maze arm. As shown in Figure 12, they retrieved the seeds at accuracy levels comparable to that reported for rats, gerbils, and mice. As shown in Figure 12, rats, hamster, and gerbils performed above chance (64%). That is, they visited more baited arms than that number of baited arms that could have been visited randomly. Chance performance was calculated by Eckerman (1980). Eckerman considers both the difficulty in discovering baited arms as the number of visits increases, and a preference factor determined by the subjects' past selection patterns when foraging with a response bias. The chance of visiting a baited arm on the first choice is 100%

Figure 12 - The percentage of visits to baited arms for rats, gerbils, hamsters, and mice. Data for rats from Olton, Collison, and Werz, 1977 ; for gerbils from Wilkie and Slobin, 1983 ; for mice from Mizumori, Rosenzweig, and Kermisch; 1982.

ACCURACY

63



since all arms are baited. This value changes for each arm selected thereafter as a function of the number of baited arms available to the subject at each selection. The reported chance level of 64% is a composite of chance performance calculated for the probability of visiting each baited arm based upon the number of baited arms available and the response biases of the subject.

Figure 13 depicts the percent of correct (i.e., as yet unvisited) arm entries, averaged across the five hamsters for Day 1 to Day 14 (i.e., accuracy across trials). In order to illustrate the comparable performance of hamsters, gerbils, and rats on the 17-arm radial maze, previously published data from gerbils (Wilkie & Slobin, 1983) and rats (Olton, Collison, & Werz, 1977) are also shown. When using a response strategy the hamsters' performance was as consistent as that demonstrated by rats and gerbils that presumably collect food rewards from the maze by using a memory-based strategy.

Arm preference ratings for hamsters (Figure 14) and rats (Olton, Collison, & Werz, 1977) (Figure 15) suggest that no particular sequence for visiting arms nor a particular arm was preferred across trials. This contrasts to that discovered for hamsters in Experiment 2. However, when the number of choices as a function of the chosen arms positions relative to the last choice is examined, a turning strategy is apparent (Figure 16). For example, choosing the arm directly to the left or right of the arm currently visited is + or - 1; choosing the arm two doors to the left or right of the arm currently visited is + or

Figure 13 - The percentage of visits to baited arms for rats, gerbils, and hamsters averaged across subjects for each trial. Data for rats from Olton, Collison, and Werz, 1977 ; for gerbils from Wilkie and Slobin, 1983.

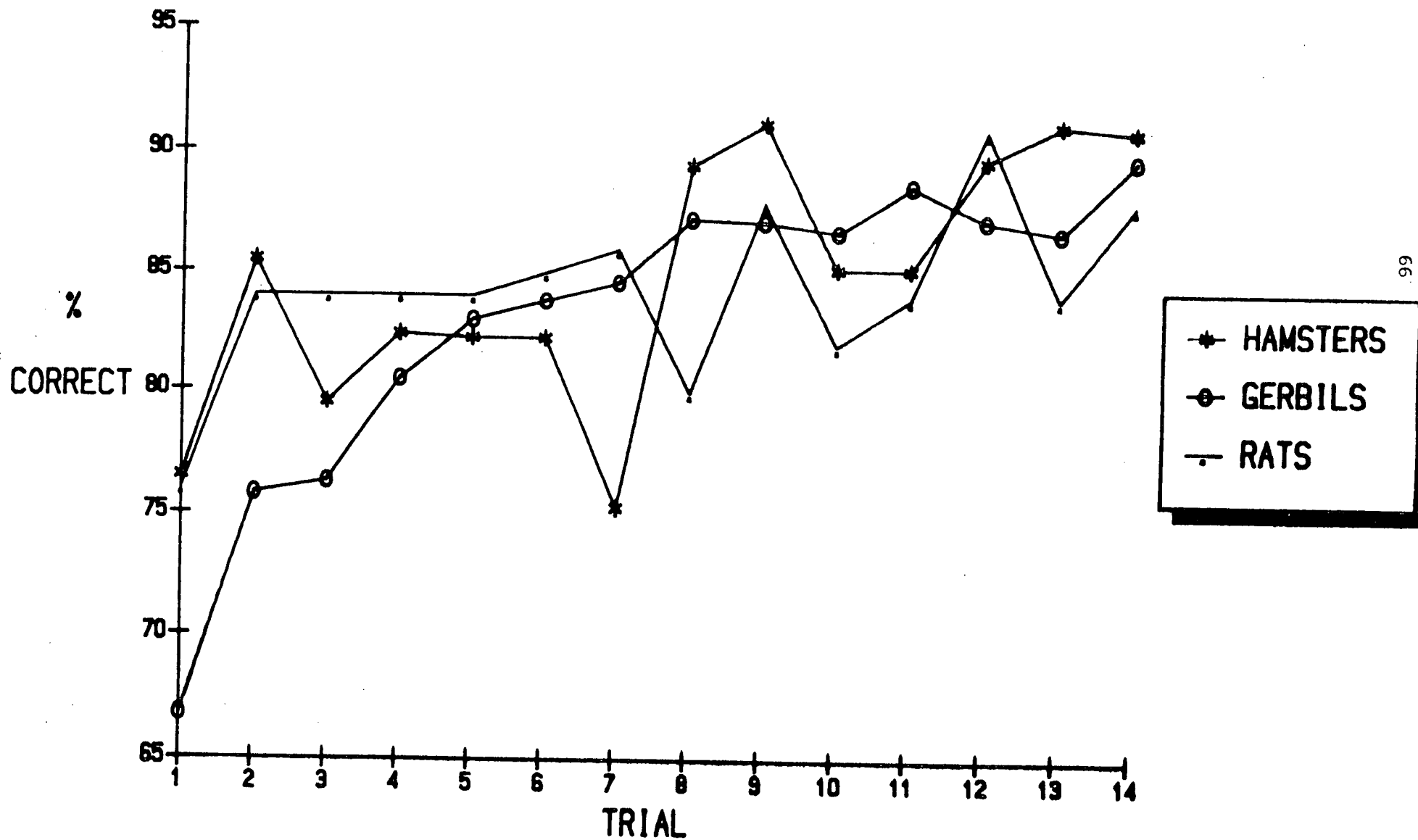
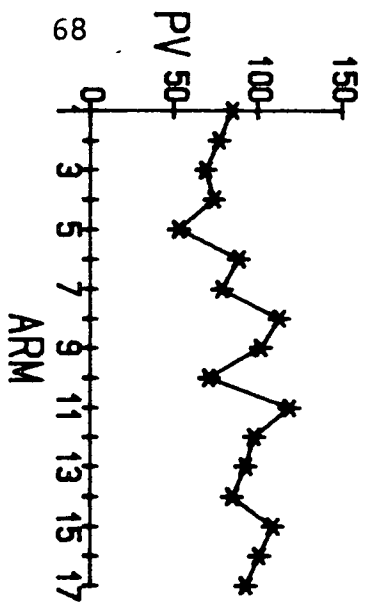
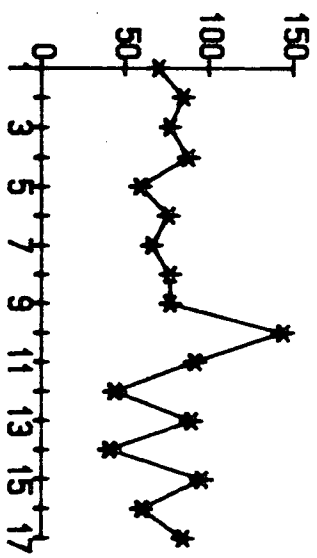


Figure 14 - The arm preference totals, preference value, summed across trials for each hamster visiting arm locations on the 17-arm radial maze.

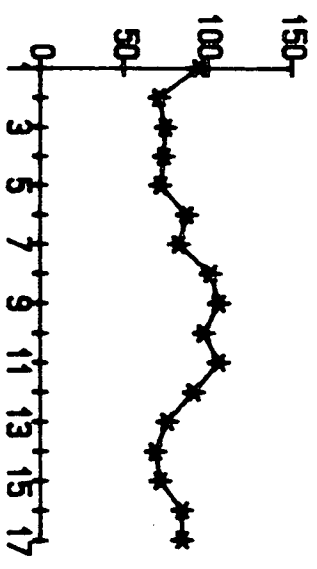
HAM 1



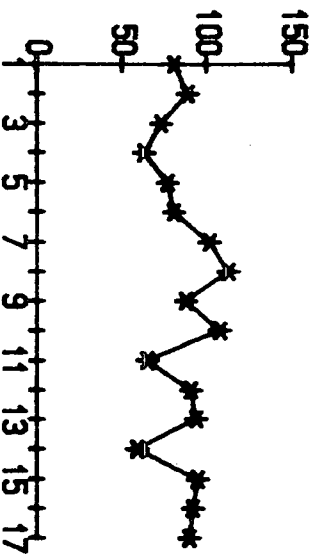
HAM 2



HAM 3



HAM 4



HAM 5

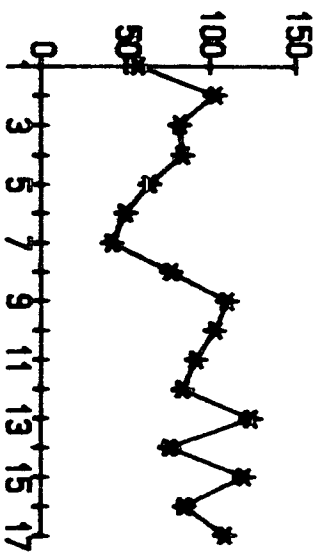
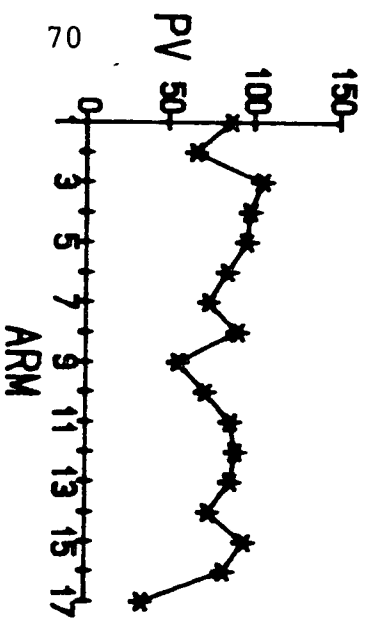
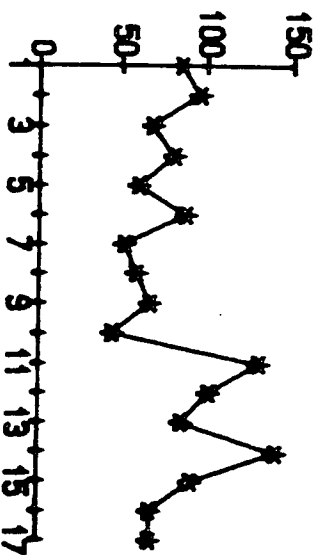


Figure 15 - The arm preference totals, preference value, summed across trials for each rat visiting arm locations on the 17-arm radial maze. Data taken from Olton, Collison, and Werz, 1977.

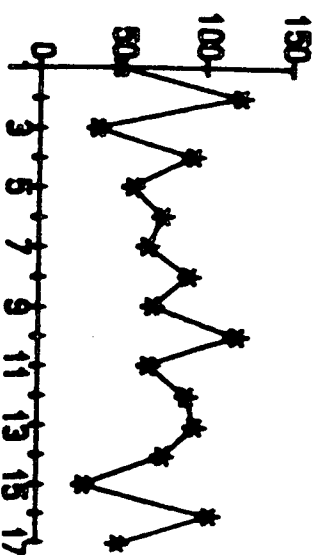
RAT 1



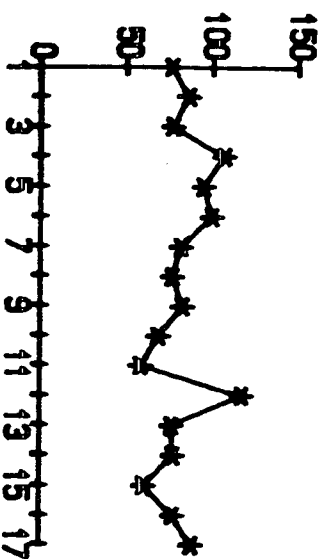
RAT 3



RAT 5



RAT 10



RAT 24

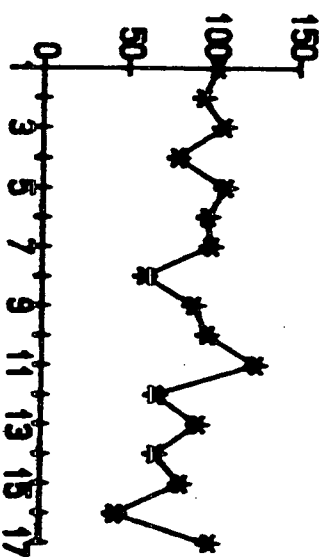
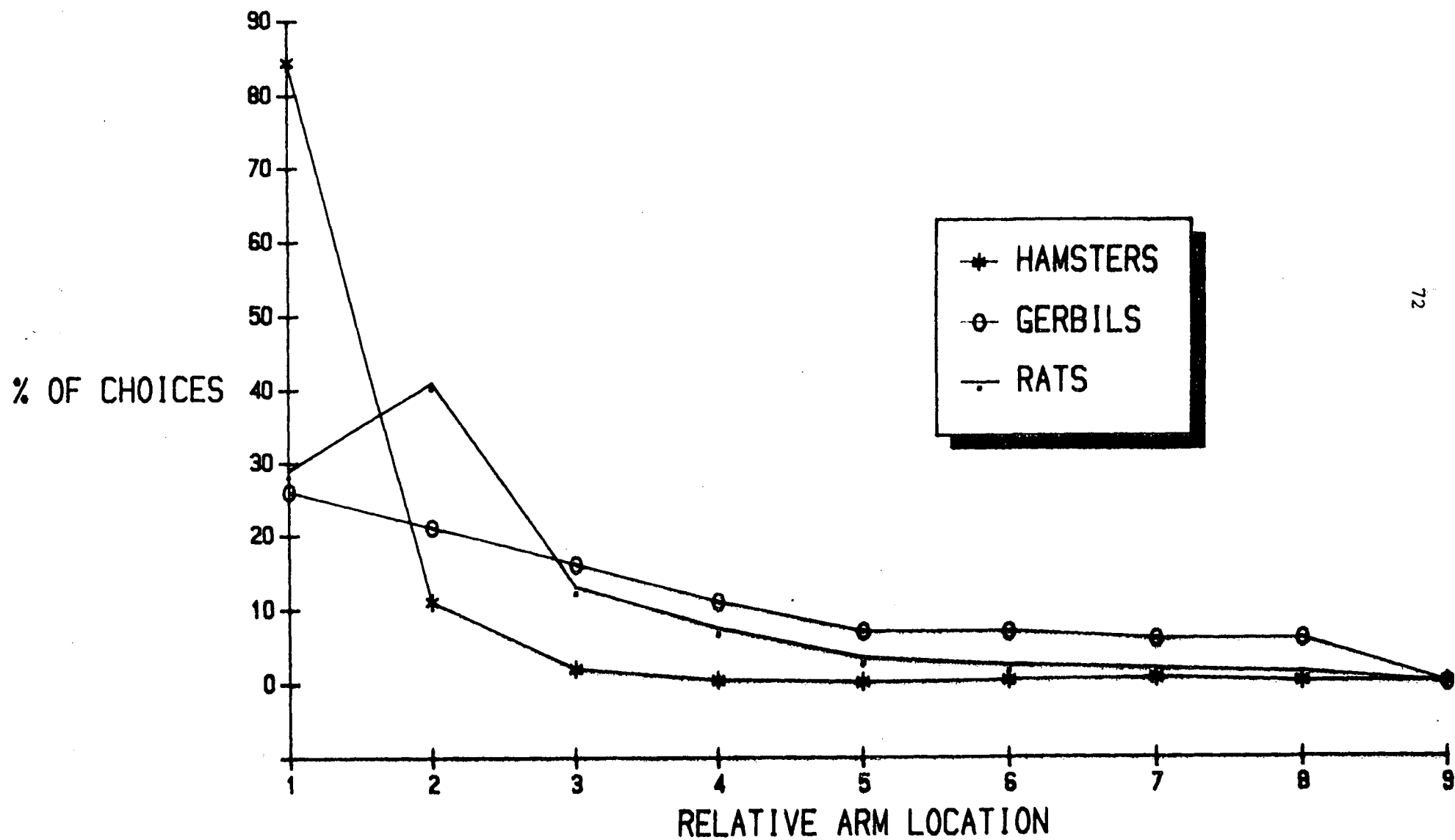


Figure 16 - The frequency of visits as a function of the arm locations relative position to the previous visit. Data for rats from Olton, Collison, and Werz, 1977 ; for gerbils from Wilkie and Slobin, 1983.

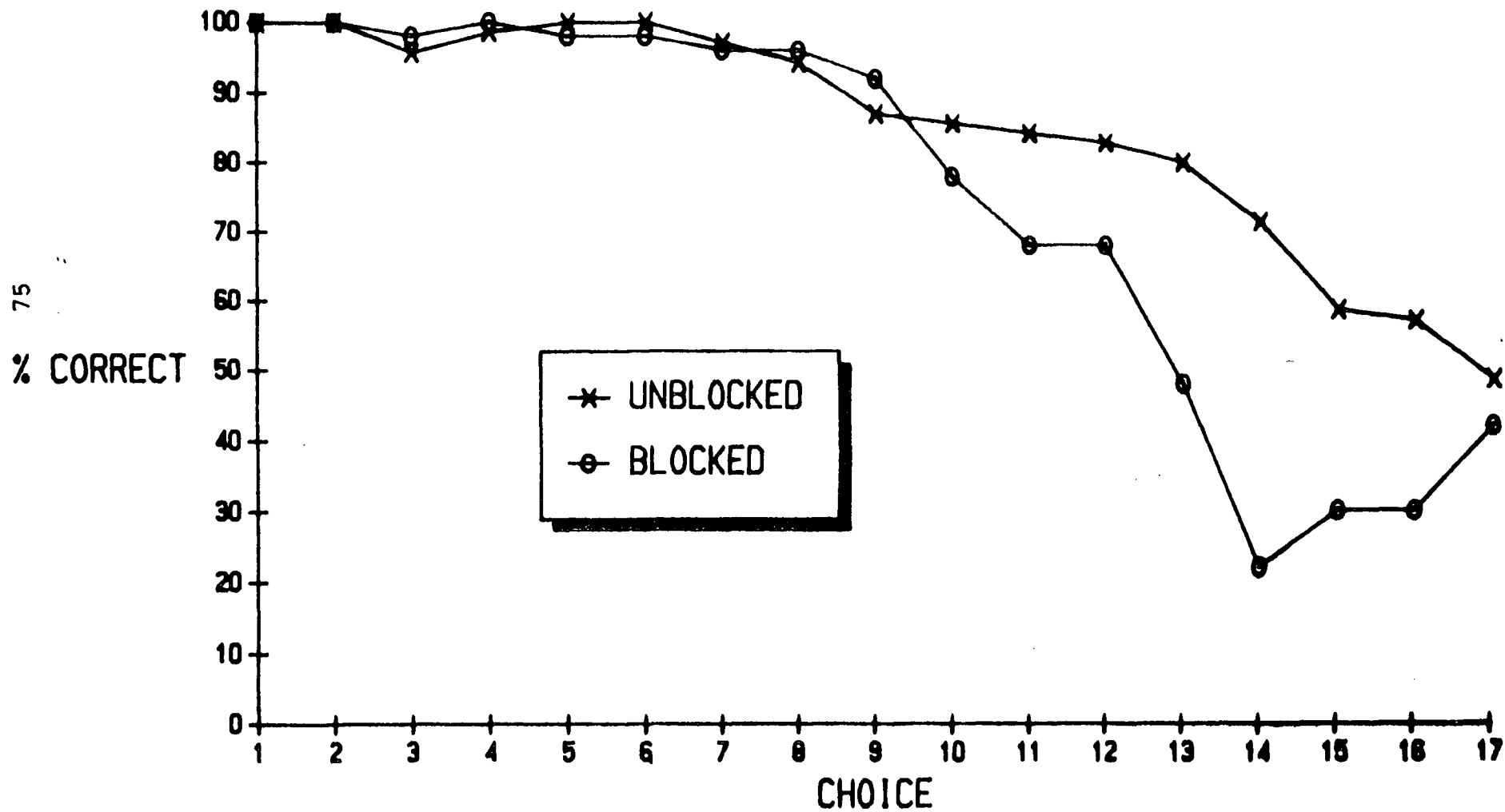


- 2; three doors is + or - 3; and so on. Thus, Figure 16 shows that hamsters choose a very high percentage of adjacent arms. Gerbils and rats, on the other hand, are much less likely to enter adjacent arms. This suggests that hamsters use a circling strategy similar to that noted in Experiment 2 when foraging on an equally baited maze.

In order to examine the possibility that hamsters could successfully choose non-adjacent baited arms when forced, a random 4 of the 17 arms were blocked. Thus, the first 13 choices forced the hamster to transverse blocked entrances breaking the response algorithm--always turn left or right. The last 4 choices forced the hamster to locate baited arms which were not adjacent. Presumably, information granted by exploration of the maze during the first 13 choices about the condition of each arm (i.e., baited vs unbaited) would be accessible during the last 4 choices.

Figure 17 compares the percent of correct choices when no arms were blocked (unblocked), and the percent of correct choices for 17 arms when 4 arms were blocked (blocked). The grand mean for the number of baited arm locations chosen by hamsters in the unblocked and blocked conditions is 84.8% and 74.4%, respectively. No difference existed between the grand mean under these conditions [$t(32)=1.29$, $p=.2100$]. However, performance decreased rapidly after the tenth choice in the blocked condition. If we compare accuracy for the last seven choices, then a significant difference between the unblocked ($\bar{M}=69\%$) and blocked ($\bar{M}=44\%$) conditions does result

Figure 17 - The percentage of correct visits to baited arms for each choice averaged across subjects in the unblocked and blocked conditions.



[$t_{(12)}=2.83$, $p=.016$]. The greatest difference between the unblocked ($\bar{M}=58.9\%$) and blocked ($\bar{M}=31\%$) conditions was found in the last four choices [$t_{(6)}=4.46$, $p=.0066$]. Thus, hamsters do not appear to possess the ability to use a memory-based foraging strategy for collecting food rewards under these experimental conditions.

Contrary to our expectations, no hamster transported seeds from the maze arms back to the centrally-located home cage. It is not clear yet why the subjects did not transport the seeds. Had more food items been available cheekpouching may have been observed.

V. GENERAL DISCUSSION

Hamsters and gerbils, like rats (Bolles et al., 1981), can identify food quality by using taste cues. In particular, these rodent species show a flavor-calorie conditioning effect. Rats and gerbils show a robust effect. Hamsters, on the other hand, are more likely to choose foods of varying quality regardless of their knowledge of flavor as a mediating cue to caloric density.

Initially, hamsters that were presented with high- and low-calorie mash did not demonstrate flavor-calorie conditioning. When hamsters were simultaneously presented with both diet mashes, they placed both mashes in their cheekpouches. Hamsters, unlike rats and gerbils, have extensive cheekpouches that aid in transporting food to the central cache. These cheekpouches apparently hindered the hamsters in forming a single flavor-calorie association. Thus, in our initial experimental task, the hamsters' cheekpouch was a biological constraint, in particular, a morphological constraint (cf. Domjan & Galef, 1983; Hinde & Stevenson-Hinde, 1973; Shettleworth, 1982).

The cheekpouch as a biological constraint in diet selection is an important consideration. A cheekpouch enables a forager to transport large quantities of food to a central nest. Thus, hamsters can harvest food and build hoards. Indeed the hamsters' use of a response strategy when foraging on the radial-arm maze may reflect a harvesting pattern. With cheekpouches, a harvester may haphazardly collect seeds that are strained through a selection process after a foraging bout.

This type of foraging suggests that the hamster may be a delayed-decision maker.

In a natural setting, central place foragers who have intense predation pressure may benefit by delaying diet selection until the risk of predation is decreased. While foraging, hamsters may load their cheekpouches quickly and nonselectively. This decreases their predation risk by economizing the amount of time spent away from cover in order to forage. Lima and Valone (1986) have shown that grey squirrels (Sciurus carolinensis) which are central place foragers will alter load size when foraging under various cover densities. Kotler (1984) suggests that the foraging behavior of granivorous desert rodents is also responsive to both predation risk and food resources. Accordingly, hamsters that forage in barren desert climates may have cheekpouches in order to safely transport large quantities of food long distances in sparsely covered areas. Thus, cheekpouching abilities increase foraging efficiency. However, in certain diet selection tasks, they may be considered a biological constraint.

Cheekpouch loading is advantageous to a highly-predated generalist feeder. However, if cheekpouches were sensitive to toxins or flavors, then the loading process may become inefficient. For presumably, a hamster discards unwanted foods, such as poisonous or decaying items, after returning to its burrow. If the hamster has to note the flavor of a food while harvesting, then the process of cheekpouching slows down the foraging process. Therefore, in our initial experimental

situation hamsters may have been unable to form a single flavor-calorie association when cheekpouching was possible. The introduction of liquid diets forced hamsters to taste each food. At this time, the flavor-calorie conditioning effect was evidenced.

Gerbils, which do not have cheekpouches, necessarily taste food that they transport to their homesite or burrow. The difference between hamsters and gerbils in hoarding strategy was clear in our experiments. Hamsters loaded their cheekpouches and transported the cheekpouch contents to the corner of the cage where they cache their food. Gerbils attempted to move the food cups but otherwise ate the mash directly from the cup. Since gerbils could not transport the mash, their immediate concern may have been food quality. Gerbils may not be delayed-decision makers. If this is the case, then the gerbils increased sensitivity to taste cues over that of the hamsters is not surprising.

The flavor use difference between hamsters and gerbils is further strengthened when we consider the extinction effects of the test phase. Hamsters, which required liquid presentation to avoid cheekpouch effects, were more likely to choose either of the isocaloric liquids whose flavors were previously paired to high- or low-calorie Sustacal. Their preference for a particular flavor was not tenacious. Gerbils, however, continued to prefer the flavor that was previously paired to the high-calorie mash. Gerbils appear to maintain a stronger flavor association than do hamsters.

Gerbils apparently use cues other than taste when choosing the high-calorie mash. In the flavors reversed and no flavors condition, no low-calorie mash was consumed. Another sensory cue, which Bolles et al. (1981) suggested that rats may have used, is texture cues. The low-calorie mash contained alpha-cellulose which is a non-caloric fiber. Thus, the low-calorie mash may have had a softer or drier texture. When the diets were mixed both isocalorie mashes necessarily had the same texture. Therefore, gerbils relied upon taste cues. Of course, gerbils also demonstrated the flavor-calorie conditioning effect when presented with Sustacal liquid. Thus, they do not rely exclusively on texture cues, but may also use taste cues. Hamsters and gerbils that consumed Sustacal liquid could not use texture cues since both the diet mixes were watered down to different consistencies; no additives were employed.

An interesting question in the flavor-calorie conditioning paradigm involves the rodents' ability to detect caloric density given the same flavor. When given two foods with the same flavor but different caloric densities will rodents be able to detect caloric density, and prefer the higher quality food item? Or, will the sweetness of both solutions inhibit rodents' from identifying the high-calorie food item. We've labelled this the "Nutrisweet dilemma". For example, if rats are presented with cherry Kool-aid that is sweetened with Nutrisweet and cherry Kool-aid that is sweetened with sugar, then which Kool-aid drink will they prefer? This approach asks if the amount of sugar in a food item can be detected without taste or texture cues. This

approach could also be used to explore the rodents' sensitivity to food items with excessive sugar. Can a food have too many calories or be too sweet?

Interestingly, we assume that since animals have an innate preference for sweet foods that they will always choose food items with the highest sugar content (Rozin, 1977). Perhaps, this assumption is faulty. As mentioned earlier, animals can eat too much of a 'good' food. Since animals must gather nutrients in addition to calories, food-search behaviors which rely exclusively on caloric input may be maladaptive. The energy maximizing model of OFT assumes that optimal equates to 'most'. Thus, if energy is defined in terms of caloric units, then foragers must eat the most amount of calories in order to appear as optimal foragers. However, the 'most' amount of sugar, for example, that an animal can ingest may be harmful. Although the body can store food in the form of fat, an overweight forager is at a disadvantage for two reasons. First, their bodies are unnecessarily taxed. Second, overweight foragers cannot flee from predators as quickly as fit animals. In light of these disadvantages for unfit foragers, perhaps the definition of an optimal forager should not be the animal who collects the 'most' energy in terms of caloric units.

When we assume in OFT that animals have no nutritional constraints, perfect knowledge of food quality and of tradeoffs with other kinds of costs or benefits (Krebs, Stephens, & Sutherland, 1983), we may not be as mistaken as when we assume optimal is the 'most'. Indeed, in our demonstration hamsters

and gerbils did have knowledge of food quality. However, when actively foraging they did not seek to maximize energy intake in the same manner as defined by OFT. Although we stress that high sugar or caloric intake is unhealthy for humans, we expect healthy or fit non-human animals to demonstrate high sugar or caloric intake. The keywords mentioned in the introduction are 'proper diet'. Rodents may have knowledge of proper diet requirements and select foods according to their nutritional needs. According to 'cafeteria' data, healthy rats can self-select a balanced diet (Lat, 1967; Richter, 1942-1943, 1955; Rozin, 1968). Experimenters, on the other hand, may not have knowledge of the rodents immediate dietary needs and set as a premium extreme and exorbitant nutritional goals for the rodent.

The feeding strategies adopted by rodents in order to maintain a proper diet may be shaped by food availability. A rodent that can hoard may react differently to scarce food. Wong (1986) suggests that hamsters and gerbils that have been food deprived may have different feeding strategies. According to Wong, hamsters will not enhance food intake when deprived. That is, they maintain the same overall caloric input per day. Gerbils, however, increase food intake when deprived. In our 8-arm radial maze situation hamsters visited all food locations, but preferred to drink from the high-calorie arm locations. Gerbils, on the other hand, seemed to randomly select arm locations and were more willing to drink from either high- or low-calorie arm locations. Since both rodents were deprived, perhaps, deprivation state had differential effects on hoarders

(i.e., hamsters) and non-hoarders (i.e., gerbils). This should be further explored by introducing a non-deprived group of hamsters and gerbils into the same experimental situation outlined in Experiment 2.

Batson et al.s' (1981) description of the rats' behavior when foraging on a radial-arm maze for a single chocolate milk reward provides an example of the rodents' change in foraging behavior when food and/or water deprived. They appear to choose foods which are needed and to avoid unnecessary foods. When thirsty rats were placed on an 8-arm radial maze with seven arms baited with water and one arm baited with chocolate milk. Their preference for the chocolate-baited arm did not change. However, when food and water deprived the rats' preference for the chocolate-baited arm increased. Thus, to a thirsty rat, the food reward was unnecessary. The rats that had knowledge of the food quality - location association used this information only when necessary.

Radial arm maze tasks have been used extensively to explore rodent foraging strategies (Mizumori, Rosenzweig, & Kermisch, 1982; Olton, Collison, & Werz, 1977; Wilkie & Slobin, 1983). Radial-arm mazes offer a unique opportunity to investigate the role of diet selection in foraging tasks under a controlled experimental situation. According to this thesis research, the rodents' ability to choose foods that provide adequate nutrients in a choice task may actually tell us very little about diet selection in an active foraging situation. Neither hamsters nor gerbils in our experimental setting sought food in a manner in

which the observer could identify the foragers' knowledge of food quality. According to our results from Experiment 1, hamsters and gerbils knew which flavor represented the high-calorie food. However, when visiting food locations this knowledge was not demonstrated. Perhaps, in an actual foraging situation where travel increases cost a larger difference in food quality is necessary before this knowledge is demonstrated. Future research should explore the rodents' arm choices given highly different food quality - flavor associations (e.g., low density contains 20% of the calories found in the high density diet). In addition, future research should investigate the rats' performance in a similar maze situation as used in Experiment 2.

Recall that Mizumori et al. (1982) suggested that the radial-arm maze situation may tell us very little about rodents' food-searching strategies. This statement was partially based on the observation that mice ran through the maze at a much quicker pace than rats. Perhaps, Mizumori et al.'s contention is correct when we attempt to compare species' performance. Indeed, in our experiments, the maze performance of hamsters may have differed from gerbils due to a foraging constraint, such as locomotion, that does not affect diet selection. For example, hamsters have quadrapedal locomotion that aids in climbing and maneuvering in bushes which yield seeds that are spatially more predictable but less dense (Rosenzweig, Smigel, & Kraft, 1975; Reichman & Oberstein, 1977). Quadrapedal locomotion allows hamsters to harvest scattered seeds more efficiently (Kotler,

1984). Gerbils, on the other hand, are bipedal and saltatorial. Their bipedal locomotion allows them both to exploit large, scattered clumps of seeds efficiently and to escape predators quickly (Kotler, 1984). As well, gerbils have enlarged auditory bullae and mastoids that allows them to detect and escape predators better than hamsters which do not have enlarged bullae. Thus, on the same radial arm maze apparatus, hamsters and gerbils may have a predisposition to move from arm to arm differently. Gerbils that use bipedal locomotion hop long distances quickly. Hamsters that use quadrupedal locomotion scurry from arm to arm surveying each possible food location in a harvesting fashion. Locomotion differences between species, as mentioned by Mizumori et al. (1982), may affect the observed foraging strategy on a radial-arm maze and should therefore be further explored.

Hamsters did not alter their foraging strategy on a larger maze. When hamsters foraged on the equally baited maze, they relied exclusively on a response or circling strategy in order to collect food rewards from the radial -arm maze. Although rats have been known to use a response strategy to collect food rewards from a radial-arm maze (Foreman, 1985), they also can locate food rewards by using a memory-based strategy (cf. Olton, 1978; Roberts, 1984). Rats collect a high number of food rewards from the maze even when interrupted by blocked arm locations or time-out sessions during which they are removed from the maze apparatus. Hamsters' performance decreased once the algorithm was disrupted by blocking arm locations suggesting

that they continued to use a now inefficient harvesting strategy to collect seeds.

Hamsters used the same response strategy of visiting consecutive arms both on the 8- and 17-arm radial maze. However, on the smaller maze each hamster began each trial in the same arm and circled the maze in the same direction. This is interesting for two reasons. First, the hamsters were randomly placed in the center of both mazes; the experimenter did not face the hamsters towards any particular arm at the start of the trial. Second, each hamster was assigned different arms as high-calorie Sustacal liquid locations. This suggests that hamsters may utilize a memory-based strategy when deciding where to begin foraging. Leger, Owings, and Coss (1983) suggest that foragers, such as ground squirrels, will use microhabitat cues as markers to initiate particular behaviors including foraging. According to Poucet, Chapuis, Durup, and Thinus-Blanc (1986), hamsters do build a representation of the environment based on topological relations between objects, the overall geometric structure provided by the arrangement of objects, and the relations between objects and extra-apparatus landmarks. Perhaps, a particular landmark was salient to all hamsters in Experiment 2. The role of habitat or environmental cues in initiating food-searching behaviors in hamsters should be further explored.

In this series of experiments, gerbils' maze performance presents an unusual case. Gerbils have shown their ability to use a memory-based strategy to collect food rewards from the

radial-arm maze (Wilkie & Slobin, 1983). But under the experimental conditions outlined in this thesis research, gerbils did not adopt a definitive strategy for visiting arm locations. Perhaps, the change in food reward from an equally baited radial-arm maze (Wilkie & Slobin, 1983) to our unequally baited radial-arm maze affected the gerbils foraging strategy or perhaps the larger maze allows a bipedal rodent to forage more efficiently. In addition, our unequally baited maze provided greater caloric input per trial than did the single 45-mg Noyes food pellets (Wilkie & Slobin, 1983) offered on the equally baited maze. Again, it would be interesting to explore the effects of increased quality differences on the gerbils' foraging performance on the radial-arm maze.

In conclusion, gerbils and hamsters did not use flavor cues that indicate caloric density as aids in locating a high calorie food source on a radial-arm maze. Both species were able to use flavor cues to detect caloric density. However, neither rodent species preferentially visited high-calorie arm locations that were marked by flavors previously associated with a high- and low-calorie food item. Hamsters, however, did prefer to drink from these sites. On both the 8- and 17-arm radial maze, hamsters located food rewards in a harvesting fashion by using a circling strategy. Gerbils did not appear to use a food-search strategy. The observed disparities between hamsters and gerbils may reflect different biological constraints (i.e., cheekpouches or locomotion), different feeding strategies at various physiological states, different interpretations of food quality,

or different food gathering strategies dependent upon the use and availability of environmental cues.

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