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Bait Shyness and Neophobia in Several Species of Osteichthyes: An Extension of Taste Aversion Studies to the Superclass Pices

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BAIT SHYNESS AND NEOPHOBIA IN SEVERAL SPECIES OF OSTEICHTHYES: AN EXTENSION OF TASTE AVERSION STUDIES TO THE SUPERCLASS PICES

by

Brent W. Roberts

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ABSTRACT

Bait Shyness and Neophobia in Several Species of Osteichthyes: An Extension of Taste Aversion Studies to the Superclass Pices

by

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Utah State University, 1978

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Three experiments were conducted with five species of tropical fish to investigate the phenomena of taste aversion and food neophobia. In addition, an experiment determined specifically if position in the tank could acquire conditioned aversive properties.

In Experiment 1, four habituated fish were fed novel meat-flavored pellets on the treatment day. Six were made ill within 30, 60, or 90 minutes (2 subjects each) by intragastric administration of syrup of Epicac. The following day all were fed familiar commercial pellets. On the second day after treatment, all were offered the meat-flavored pellets. Results showed longer latencies, more tasting, and decreased consumption of novel pellets. All measures differed significantly for the treatment subjects compared to their own baseline and controls.

Experiment II demonstrated food neophobia in four inexperienced fish. After habituation they were fed novel meat-flavored pellets but not made ill (day 0). On day 1 and 2 they received familiar diet and were made ill after the feeding on day 2. On day 3 they received familiar food again and no change in approach latency, testing response,

or quantity consumed occurred. On day 4 they were offered the novel meat-flavored pellets which they refused. These results indicate that the fish associated the illness with the more "novel" food even though their familiar diet was temporally closer to the illness.

In Experiment III five species of naive fish were habituated to 20-gallon tanks and made ill after eating in one end and not in the other. The same food was used in both ends. The "illness end" could have taken on discriminitive properties and food consumption there should have decreased, as opposed to the other "safe end". The results indicated that "place" did not acquire aversive discriminitive properties. Food consumption decreased in quantity, food approach latencies increased and length of tasting bouts increased in both ends.

These experiments were the first to use these species of fish in this type of research. The results extend the phenomena of taste aversion and food neophobia. In addition, Experiment III systematically replicated the hypothesis of relevant relations between stimuli and showed that it is easier to learn certain consequences with certain cues than with others. In this case illness was quickly associated with taste but "place" was treated as irrelevant.

(79 pages)

CHAPTER I

INTRODUCTION

It is impossible to discuss taste aversion without touching on its significance to learning theory. Most researchers use the phenomenon of taste aversion in an attempt to prove points in philosophical arguments. If not informed as to how taste aversion data applies, the reader might not understand the significance of statements like "the laws of learning are not the same for all animals"; "Pavlov, Skinner and traditional learning theorists were wrong on equipotentiality"; and "the 'belongingness', 'stimulus relevance' and 'preparedness' phenomena demonstrate that the equipotentiality premise is archaic."

When an animal eats a substance and gets sick afterwards, it tends to avoid that substance in the future. This process defines taste aversion. Neophobia is defined as "new object reaction." Specifically, in reference to taste aversion research, neophobia refers to the initial reluctance to ingest much, if any, of a novel food. This reluctance occurs to new foods in general and does not have to be associated with illness. This is in contrast to the special case involving specific hungers where new food is presented to an animal which has been on a deficient diet which has made it ill. In this case the animal shows "neophilia", which is most probably an aversion to the old diet that has made it sick, but which means prefering the new.

Specifically, neophobia refers to the ability of an animal to associate an illness with a new food recently ingested even when familiar tasting foods intervene, and are in fact temporally closer to

the illness than the novel food. For example, if five different foods are ingested before an illness is induced, one novel and the other four familiar, a rat will avoid the novel food and not the others. This it will do even though the four familiar foods were ingested at the same meal, or even after the novel food, and are therefore closer in time to the illness.

Specific Hungers and Learning Over Long Delays

Research on specific hungers started long before taste aversion studies. With this phenomenon an animal learns to prefer the flavor of a food which it eats just prior to the onset of favorable consequences. The flavor, therefore, becomes associated with getting better. What is significant here is that these associations between flavor and illness occur over very long delays with many intervening exteroceptive stimuli.

Traditional learning theories postulate that such procedures should confuse the animal into associating the "illness" or "getting better" with the very last event before the consequence. However, this does not occur. Residual taste explanations have been discredited as have other attempts by traditional learning theorists to minimize the significance of the finding that learning can occur over very long delays.

Stimulus Relevance and the Equipotentiality Premise

The phenomenon of learning over long delays leads to the issue of stimulus relevance, belongingness and the preparedness phenomenon--

that is, the animal's tendency to associate stimuli, (e.g. tastes), with certain consequences, (e.g. illness), rather than associating either tastes or illness with anything else. There appear to be built-in tendencies to associate certain categories of stimuli with certain events as opposed to other events. The consequence of becoming ill is associated with ingestion of a novel-tasting food rather than blinking lights for example, since the illness is relevant to the taste of the food and is irrelevant to blinking lights. Gastrointestinal and related internal events are more likely to be associated with substances eaten and their taste, than are "place" or exteroceptive stimuli. The equipotentiality premise, that responses to any stimuli can be readily conditioned by any type of a consequence, is not supported by taste aversion research. The equipotentiality premise holds that, for example, in classical conditioning, the choice of CS and UCS does not matter and that all CS's and UCS's can be associated more or less equally well. In addition, general laws exist which describe acquisition, extinction, inhibition, delay of reinforcement, and spontaneous recovery for all CS's and UCS's. The choice of response and reinforcer is said to matter little in instrumental learning also. Any emitted response and reinforcer can supposedly be associated about equally well and general laws exist here also.

Learned Safety

Tastes are linked to gastrointestinal events and there is usually an inherent long delay in that system. Rats, after consuming a novel food, and in the absence of unfavorable gastrointestinal events, as time passes, learn that the solution or food they ate is safe. This

is demonstrated by the fact that it is difficult to develop in a rat a taste aversion toward a food with which it has had many encounters where unfavorable consequences did not occur. That a particular tasting solution is "safe" (not followed by unfavorable consequences) in one compartment and "unsafe" (always followed by illness) in another is not an easy association to make for the rat. Places in the environment do not associate easily with sickness.

Origin and Statement of the Problem

It is well known that many animals, man included, avoid foods which have been associated with illness. This phenomenon occurs even if the illness is induced by X-ray (Garcia & Kimeldorf, 1960; Garcia, Kimeldorf, & Koelling, 1955), or drugs (Garcia & Koelling, 1967) and occurs hours after the food item has been consumed. It has been assumed by some that the aversion comes about because the animals somehow associate the taste of the food with the sickness that follows (Garcia & Koelling, 1966, 1967b). This assumption questions the traditional Pavlovian paradigm which demands nearly immediate CS-UCS pairing for conditioning to occur. Taste aversion occurs even when there are many intervening stimuli between consumption of food (CS) and subsequent illness (UCS).

There is disagreement concerning the conclusions of taste aversion experiments. Some authors contend that backward respondent conditioning can occur and others say it does not (Boland, 1973). Some experiments have shown that of two novel substances, taste aversion was established only to the more "palatable" of the two, while others argue that the most preferred is not the most avoided but the other way around (Etscorn, 1973).

Neophobia, or "new object reaction," may be evoked in rats when unfamiliar objects are in familiar places or when familiar objects are in new places. In the case of food, rats avoid ingesting new items in familiar or unfamiliar places. This avoidance is temporary and the rat may soon come to eat even more of the formerly unfamiliar food than its familiar diet. Gastrointestinal distress and electric shock differ in effectiveness as UCS's in controlling drinking behavior in rats. Such "stimulus relevance" is supposedly due to different physiological mechanisms governing the association between taste and illness and between taste and shock (Green, Leonard, Bouzas, Arturo, & Rachlin, 1972). It has been suggested that there exists a neurological center where taste is easily associated with visceral but not with peripheral cues (Garcia, McGowan, & Green, 1972).

It is clear that rats and other animals utilize gustatory cues to avoid food items that previously made them ill. There is, however, no evidence that they avoid the "place" where any particular toxic food item was consumed (Garcia & Koelling, 1966). But had the rat received electric foot shock in a certain place it would avoid that place. The role of peripheral cues, such as lights and geographical places, differ from gustatory cues in their ability to acquire conditional stimulus properties. "Apparently stimuli are selected as cues dependent upon the nature of the subsequent reinforcer," (Garcia & Koelling, 1966, p. 123). In Garcia and Koelling (1966) distress was induced by toxins or shock (UCS) while taste or audiovisual stimuli were the CSs. Results indicated that illness was associated with taste and not with the audiovisual stimulus, whereas

shock was associated with audiovisual cues and not with taste. This finding seriously questions the equipotentiality of reinforcers premise which states that any given reinforcer is equally effective for all classes of discriminable stimuli. It is speculated that natural selection has favored mechanisms which associate illness with taste as opposed to illness with place, and pain with exterocceptive stimuli rather than interoceptive, such as taste. Evolution appears to have prepared some "connections" and not others. Whether lights, or places, can acquire conditional stimulus properties with fish, when the UCS is illness, is one of the major areas of concern of this thesis.

Objectives

The purpose of this thesis is to conduct research regarding the nature of taste aversion existence in fish. The study will also shed light on the critical parameters of this process.

It is hypothesized that fish will acquire aversions to the taste of certain food items in much the same way as rats. In extending the study of taste aversion to another species it is hoped that more will be understood about the general nature of the phenomenon and its broader implications in the animal world. The results could also have application in the field of game management to aid fisheries biologists in understanding more about problems in the hatchery and angeler's problems on lakes and streams. Results should also be interesting to tropical fish farmers who lose many exotic species due to eating problems.

The objectives of this study are:

1. To extend the study of bait shyness to a selected species of tropical fish.

2. To determine the presence or absence of food neophobia in this species.

3. To determine if exteroceptive stimuli, such as places, can acquire conditional stimulus properties where eating responses are the behaviors to be modified.

CHAPTER II

REVIEW OF LITERATURE

This section is presented in five parts which corresponds to a chronology of the taste aversion literature. Early statements resemble what Seligman proposes as "preparedness" (Seligman, 1970), Garcia and Koelling call "belongingness" (Garcia & Koelling, 1966) and, Capretta calls "stimulus relevance" (Capretta, 1961).

The second period begins when Garcia and colleagues working on radiation studies steming from the radiation scares of the 50's and 60's all but stumbled on to the taste aversion phenomenon. Much classic work on taste aversion came between 1960 and 1968. Reviewers writing between 1968 and 1972 comprised phase four.

From 1972 to the present is phase five. Minor details are now being argued (e.g. Barnett, 1958 vs. Mitchell, 1976). More weighty issues are debated by Skinnarian behaviorists who think these rebels have gone too far and have little evidence; their "learning over long delays" can be explained in other ways. The ethologists (e.g. Bitterman, 1975) on the other hand, applaud, but feel enough has not yet been done to demonstrate evolution's role in "prewiring" an animal. To them, it is not surprising that a rat does not pay attention to which part of the cellar the poison was in that made it sick, but rather the taste of the poison. Place is irrelevant for some associations while taste tells of life or death. However, if a rat painfully pulls its leg out of a trap in a particular tunnel then place is relevant and the "connections" are set up to avoid the tunnel.

Taste aversion research is the tool by which many cogent theoretical issues are being debated today. For example, taste aversion studies demonstrate learning over long delays and, as mentioned, is still a thorn in the side of traditional learning theorists. The "preparedness" and "equipotentiality" controversy is fueled by taste aversion research.

Period One

Much of the early work, that was later seen to be relevant to taste aversion research dealth with specific hungers. Richter (1943) showed that animals would choose a diet containing a particular nutrient which they were lacking. Rats suffering a deficiency can learn which food "made them better" and quickly come to prefer it (Harris, Clay, Hargreaves, & Ward, 1933; Scott & Verney, 1947).

Scott and Verney (1947) also provided evidence for learning in the specific hunger problem. They provided rats both a flavored, vitamin enriched food and an unflavored, deficient food. After the rats showed a preference for the flavored, fortified food, the flavor was switched to the deficient diet and the rats then preferred the now flavored but deficient food.

There were many studies on specific hungers which have lately been related to taste aversion (Rozin & Kalat, 1971). Those studies imply that the illness brought about by a deficient diet is analagous to the illness induced by lithium chloride after consuming a certain flavor in taste aversion studies. Just as the rats avoid the flavor that "made them ill", they also avoid the deficient diet that poisoned

them over the long term. Rats on a deficient diet show neophilia to new diets, even if the new diets are also deficient.

Learning over long delays. Long-delay learning and its occurance in the taste aversion phenomenon was first mentioned by Pavlov in 1927:

> This experiment provides a clue to the well-known fact that dogs will eat meat the first time it is offered them, after removal of their parathyroids, or after an Eck fistula and tying of the portal vein, but on all subsequent occasions will refuse it. Evidently in these cases the appearance and smell of meat produce of themselves a reaction identical with that produced through direct pathological action in the absence of the parathyroids or the portal circulation, by those toxic substances resulting from digestion of the meat (Pavlov, 1927, p. 36).

Also, as related by Rozin and Kalat (1971) there were others who recognized the phenomenon of long-delay learning in the literature on poisoning, regulation of food intake and, specific hungers (Harris, et al, 1933; Rzoska, 1953; Scott & Quint, 1946).

Neophobia

Neophobia, which generally means the avoidance of any novel stimuli, e.g. food, place, lights, noises, etc., is mentioned in early works of many authors (Hebb, 1946; McDougall, 1908; Small, 1901). Barnett (1958) and (1963) gives a detailed account of food neophobia in the rat. Even though one of these publication dates is post-Garcia it is still pre-Garcia in approach.

Preparedness

Concerning the idea that some responses are more easily associated with certain stimuli than others (discussed later under "preparedness" (Seligman, 1975), "stimulus relevance" (Capretta, 1961), and "belongingness" (Garcia & Koelling, 1966)), Thorndike mentions in Animal

Intelligence "... the readiness of the response to be connected with the situation," which implies that some stimuli associate better with certain behaviors than others (Thorndike, 1911).

Bait Shyness (Taste Aversion)

One of the first direct references to bait shyness was Rzoska in 1953. He demonstrated that rats need only a single exposure to a toxic food to learn to avoid it. In the period of time just after consuming a new food the contents of the food act on the body. Anthropomorphizing, it is as if the rat is standing by during this critical interval waiting to see if it feels good or bad. If it gets sick it will cease eating and (if it recovers) it will not eat that particular food again. In these situations at least two aspects help the rat. It eats very little of the new food to begin with, due to neophobia, (new food avoidance), then, if made ill, the phenomenon of bait shyness (or taste aversion) is demonstrated. If no illness follows a kind of "learned safety" process ensues.

Chitty (1954) demonstrated the protective effect of avoiding new objects, sampling, waiting, and learning to reject harmful foods. There is a stage of total avoidance of a new food followed by a tendency to sample it. All this is reviewed in Barnett (1963) in a well written chapter on feeding behavior in rats.

Period Two

During this period modern discussions of neophobia, learning over long delays, specific hungers and stimulus relevance vs. equipotentiality arose.

In the process of their work on radiation and its physiological effects on rats, Garcia, Kimeldorf, and Koelling (1955) discovered an important phenomenon. Before irradiation, rats preferred sacchrin-flavored water to plain water. The rats were allowed to drink saccharin water for six hours while being bombarded with gamma rays. After irradiation there was a preference for the unflavored water and this preference persisted more than a month. Surprisingly, this finding did not make news among students of learning theory. It was not considered very significant at the time.

This article was followed by several others (Garcia & Kimeldorf, 1957; Garcia, Kimeldorf, & Hunt, 1957; Garcia, Kimeldorf, & Hunt 1956; Garcia, Kimeldorf, Hunt, & Davies, 1956) which were not published in the prestigous journals of learning theory. Many reviewers considered the data unremarkable. Avoidance of foods that had undesirable consequences was not new. In addition, Garcia's work was considered applied research and therefore not applicable to academic, theoretical subjects.

With further research the relevance of learning theory became evident. At the end of period two, or the beginning of period three, the classics of William A. McLaurin (1964); Garcia and Koelling (1966); Garcia, Ervin, and Koelling (1966); and Smith and Roll (1967) were published.

In 1961 Garcia, Kimeldorf, and Hunt published a paper essentially advertising their findings, but still weighted toward radiation research. It mentioned that the taste aversion paradigm essentially followed traditional classical conditioning lines but that the interval between drinking the flavor (CS) and the irradiation treatment

(UCS) was measured in hours rather than seconds. He does not say anything about that being a bit odd. There is also evidence that with X-ray treatment, as the UCS, there is a learned avoidance to the place where irradiation occurred. This avoidance of place is not found when chemicals, such as lithium chloride, are used as the UCS (Garcia, Ervin, & Koelling, 1966).

Capretta (1961) concluded:

> That food preference can be reduced by pairing the consumption of a specific food with noxious alimentary states such as result from salt-water loadings (Capretta, 1961, p. 242).

The interesting aspect of this study is that color and not taste was used as the CS. Wilcoxon, Dragoin, and Kral (1971), demonstrated that rats make use of taste while some quail can use visual cues, visceral and peripheral respectively. So, with rats, gustatory cues are appropriate when learning of food's consequences while with quail, visual cues are dominant. This seems logical considering their different feeding patterns, nocturnal vs. diurnal.

Periods Three and Four

These will be considered together since the general reviews of the fourth period are used as a guide to the third. The most complete reviews are Hinde and Stevenson-Hinde (1973); Revusky and Garcia (1970); Rozin and Kalat (1971); Seligman (1970); Seligman and Hager (1972); and Shettleworth (1972).

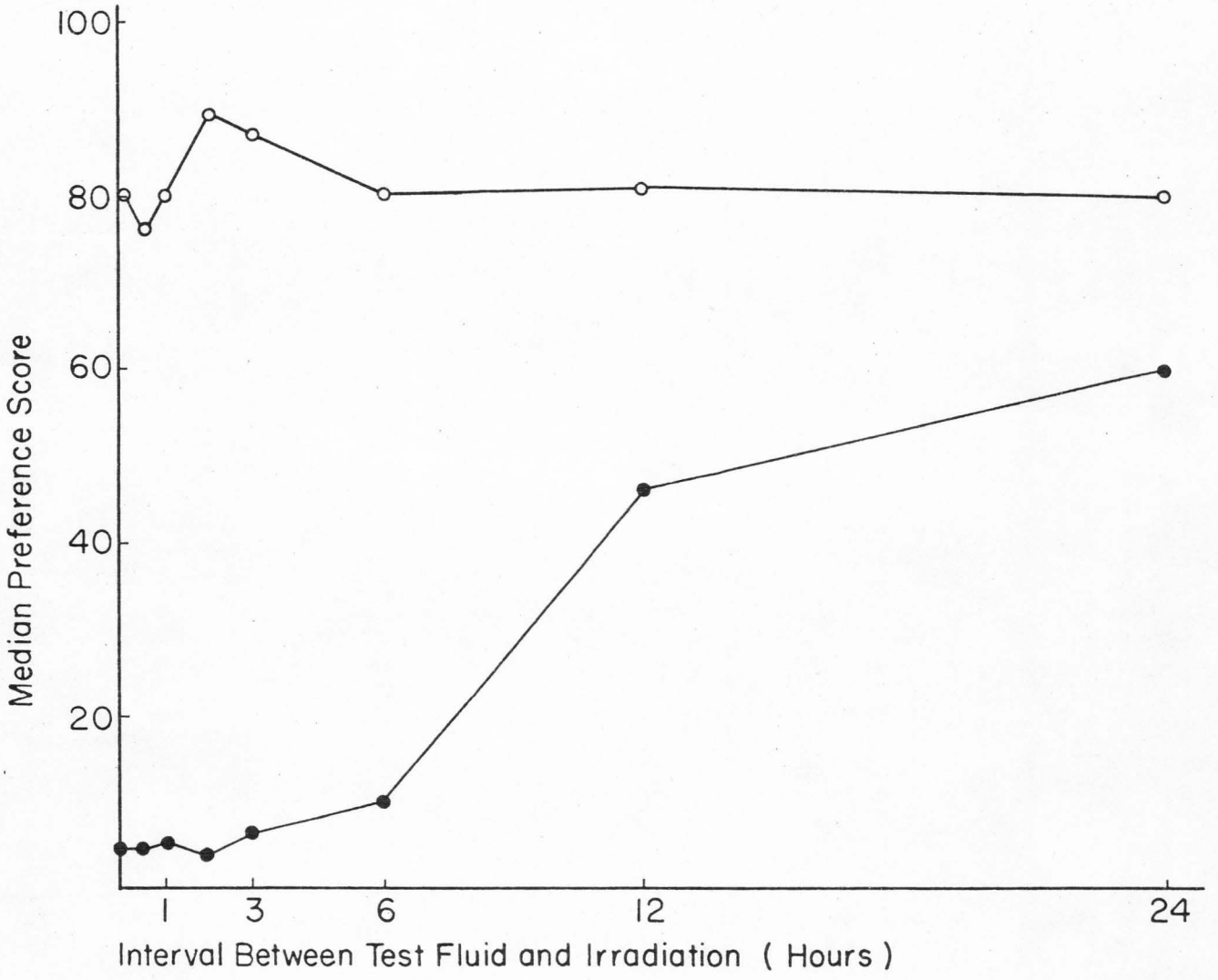
Taste aversion. The significance of taste aversion studies lie in what this phenomenon means in terms of explaining the theoretical issues of preparedness vs. equipotentiality, long delay learning, etc.

By itself, what happens in taste aversion is simply explained. What happens is easy, but how and why have not yet been satisfactorily handled.

Smith and Roll (1967) typifies the work in taste aversion at that time. Deprived of liquid for 24 hours, rats were given access for 20 minutes to a saccharin solution. X-ray, or sham exposure, for 200 seconds was then administered after 0, .5, 1, 2, 3, 6, 12, or 24 hours. The results are shown in Figure 1. The interesting point is that even with 12 hours between the saccharin (flavor) and irradiation (illness inducing) the animals subsequently showed an aversion to saccharin. These findings have been confirmed by many others (Garcia & Kimeldorf, 1957; Garcia, Kimeldorf, & Koelling, 1955; Smith & Morris, 1963; Smith, Morris, & Hendricks, 1964) and are not in accordance with findings examining other types of learning where the delay interval was measured in seconds, e.g., passive avoidance (Baron, 1965), escape (Fowler & Trapold, 1962), and reward (Grice, 1949).

While ionizing irradiation was initially used as the UCS many drugs have been shown to be effective in producing aversion, in varying degrees, among which are lithium chloride (Nachman, 1963), apomorphine (Garcia, Ervin, & Koelling, 1966), d-amphetamine and mescaline (Capell & LeBlanc, 1971), ethanol (Lester, Nachman, & LeMagnen, 1970), cyclophosphamide (Garcia, Ervin, & Koelling, 1967), morphine and chlordiasepoxide (Capell, LeBlanc, & Endrenyi, 1973), cyclohexamide (Booth & Simpson, 1973), formalin (Woods, Weisinger, & Wald, 1971), methyl mercury (Braun & Snyder, 1973), anesthetics (Brown & Glusman, 1971), isotonic saline administered intravenously

Figure 1. Median preference scores for each delay condition for control (open circles), and experimental (closed circles) subjects. From Smith and Roll (1967).


100
80
60
40
20
Median Preference Score
1
3
6
12
24
Interval Between Test Fluid and Irradiation (Hours)

(Revusky, Smith, & Chalmers, 1971), hypertonic saline (Hargrave & Bolles, 1971), and p-tetrahydrocannabinol (Elsmore & Fletcher, 1972).

Revusky and Garcia (1970) found that 100 roentgens of ionizing radiation is more effective in establishing taste aversion than apomorphine injections, which make the animal very ill in a dose of 10 mg/kg. This was also noted by Barker and Smith (1974) who found that irradiation could be used to induce taste aversions if administered prior to consumption of the saccharin solution--a backward conditioning design. These results could not be obtained when lithium chloride was used in backward conditioning while both X-rays and lithium chloride were effective if administered after consumption of the saccharin solution.

The severity of the illness produced by drugs is related to dosage. As shown by Revusky, aversion increases as severity of irradiation increases (Revusky, 1968). Garcia, Ervin, and Koelling (1967) noted a similar dose-dependent effect using illness-producing nitrogen mustard injected intraperitoneally.

The degree of preference decline for a test substance is related directly to the amount of illness those solutions, which are associated with the tastes, produce. This finding is analogous to passive avoidance studies which show that suppression of an instrumental response is a function of the shock intensity.

There is a question, however, whether illness is necessary at all in the production of taste aversion. The "sickness" which arises from irradiation at low doses is inferred by the results (the developed aversion for the test substance) and not from observable signs and symptoms (Garcia & Ervin, 1968). Irradiated animals have none of the

signs of drug-treated animals. Lithium chloride produces marked inactivity, diarrhea and decreased fluid intake, and painful stimuli, such as shock, cause excessive urination, defecation and squealing, none of which is seen with irradiation. Besides radiation, Berger (1972) has shown that aversions can be produced by injections of scopolamine, amphetamine, chloropromazine and benzodiazepine in moderate doses, and none of these produce obvious signs of illness. So, as far as Berger is concerned, "... sickness is not a necessary precondition for the development of conditioned food aversions" (Berger, 1972, p. 25). Others contend that even though signs were not obvious, it is hard to imagine that irradiation or the drugs mentioned did not cause some discomfort to the animal. For a complete review of this issue see Nachman and Hartley (1975).

Out of this work another interesting question has arisen. The question relates to novel vs. familiar foods. Why does the animal associate illness with one taste as opposed to another? Given two or three foods to choose from at one time before illness is induced, one being totally new and the others very familiar, the animal will sample them all, eating more of the familiar ones. After illness is induced and recovery occurred, the animal will totally avoid the previously new food and eat the familiar ones as if nothing had happened. This occurs even if the new food is eaten prior to the familiar foods such that they are interposed between the illness and the new food (Roberts, 1973). Revusky and Bedarf (1967) showed that the most novel of two foods was more strongly associated with toxicosis.

Such findings demonstrate the role of neophobia in arranging the critical associations in a manner that might best benefit the animal in its quest for survival. Traditional learning theorists would say that the last food ingested, novel or not, would be the one more strongly associated with illness. This is not the case. Wittlin and Brookshire (1968), among others, have replicated Revusky and Bedarf's findings. Siegel (1974) showed that a single pre-exposure to a novel flavor retarded aversions compared with no exposure prior to the experimental associative ingestion. One pre-exposure to either coffee or vinegar flavor retarded the learning of an aversion when later associated with lithium chloride.

Kalat in 1974 seems to have the last word on a long debated problem of the "salience" of novel solutions and subsequent strengths of aversions. In summary, he contends that the strength of the association between a novel taste and illness depends little on the "strength" or concentration of the flavor but rather on the degree of novelty or unfamiliarity of the taste. These findings oppose Green and Churchill (1970), and Sutker (1971), who suggest that salience corresponds to palatability, and Dragoin (1971), who agrees with Hull's stimulus intensity dynamism principle (Hull, 1971), that the stronger the stimulation (strength of solution) the stronger the aversion.

Taste aversion studies often use rats as subjects, however, taste aversion work has revived comparative psychological studies and many other animals have been used: avian species (Capretta & Moore, 1970; Wilcoxon, Dragoin, & Kral, 1969), rats (Kalat & Rozin, 1970), guinea pigs (Kalat & Rozin, 1970), monkeys (Garry & Ober, 1970), and reptiles

(Burghardt, Wilcoxon, & Czaplicki, 1973). At the time the present research was completed there had been no publications dealing with fish, however between completion of the research and this writing there have been two articles using Cod (Gadus marhus) as subjects (MacKay, 1977, 1974). There have also been recent studies with coyotes and other predators by Garcia and colleagues (Brett, Hankins, & Garcia, 1976; Ellins, Catalano, & Schechinger, 1977; Gustavson, Garcia, Hankins, & Rusiniak, 1974; Gustavson, Kelly, Sweency, & Garcia, 1976; Rusiniak, Gustavson, Hankins, & Garcia, 1976).

Specific Hungers and Poison Avoidance

This topic represents the other half of the taste aversion phenomena. An animal on a deficient diet is, in essence, slowly being poisoned and that diet gradually becomes aversive to the organism. When a new tasting diet is offered, even if it too is deficient, the animal will switch. Rats reliably seek out new diets which may not be deficient in thiamine or riboflavin for example. Just as lithium chloride can be associated with a particular taste, or diet, so can the animal's failing health be associated with a particular diet.

This phenomenon was made easier to understand when taste aversion studies demonstrated the phenomenon of learning over long delays. How the animals could develop a clear preference for a thiamine rich diet over a deficient diet was a little easier to understand. Currently one cannot discuss the study of specific hungers without referring to the contribution of taste aversion research. Since reviewing each article concerned with the development of this subject, and its relationship with flavor aversion research, would be impossible,

the interested reader should refer to the excellent review of Rozin and Kalat (1971).

Taste Aversion Learning: An Example of Adaptive Specialization of Learnings (Rozin & Kalat, 1971)

The significance of taste aversion studies is demonstrated nowhere better than in the course of discussing stimulus relevance vs. equipotentiality and long-delay learning. Without doubt, the finding that delay intervals could be measured in hours rather than in seconds was disturbing for many researchers. Traditional learning theorists thought in terms of seconds with regard to CS and UCS pairing. Close temporal contiguity was necessary and all but taken for granted with apparent exceptions really depending on secondary reinforcement (Kimble, 1961). Deitz and Capretta (1966) provided a general explanation they called "stimulus relevance" which stated that the associative strength of a cue or stimulus with some consequence depends on the nature of the consequence. This means that exteroceptive stimuli will be most likely to gain high associative strength with external, peripheral consequences and, interoceptive stimuli are likely to obtain high associative strengths with internal, visceral consequences. These basic ideas are also held by Garcia and Koelling (1966) as "belongingness", and Seligman (1972, 1970) as "preparedness". Revusky and Garcia (1970) have written,

> If an animal wants to decide what made it sick, it will tend to ignore external events and carefully consider the flavors of previously consumed substances; if it wants to decide what produced an external event, it will tend to ignore flavor and will carefully consider the preceding exteroceptive stimuli (Revusky & Garcia, 1970, p. 22).

The principle of stimulus relevance states that there is a relevance between flavors and toxicosis and if irrelevant stimuli from external receptors are used in the conditioning paradigm the associations will be made much less rapidly, if at all. Flavor, with shock as a consequence, does not lead to an aversion, while pairing lights, or place, with toxicosis does not lead to avoidance of the place or lights (Garcia, Hankins, & Rusiniak, 1974). The classic report by Garcia and Koelling (1966) using "bright, noisy" water and "tasty" water indicates that given reinforcers are not equally effective for all classes of stimuli. The cues the animal selects from the many possible in a learning situation appear to be related to the consequences of the subsequent reinforcer. The belongingness principle in relation to taste aversion learning is elaborated by Garcia and Ervin (1968), Seligman (1970), and Shettleworth (1972).

Another interesting aspect of this work concerns the finding that various avian species make associations better when illness is the consequence of visual cues, rather than taste (Brower, 1969; Wilcoxon et al, 1971). Birds avoid toxic or unpalatable insects and if this were not so the Viceroy butterfly would be no better off with its mimicry of the toxic Monarch butterfly. This narrows the field to eating-related cues whether they be visceral or peripheral, and that taste-poisoning belongingness must give way to whatever modality is primary by the particular species (Rozin & Kalat, 1971). It is hoped, by applied workers in the field of predator control, that some visual eating-related cues do figure in the paradigm. Coyotes, having eaten poisoned lamb and made ill, hopefully will avoid lambs in the future

"on sight", and not on "taste" alone, since the lamb would have to be killed in the latter case.

Long Delay Learning

It has been thought impossible for learning, in either the classical or operant paradigms to occur with delays of reinforcement exceeding a few seconds. Close temporal contiguity was traditionally considered essential. McLaurin (1964) was the first to systematically manipulate CS-UCS intervals over a wide range in taste-aversion learning. Garcia, Ervin, and Koelling (1966), avoiding a technical mistake made by McLaurin, successfully demonstrated learning with delays of reinforcement on the order of one hour. Smith and Roll extended the phenomena to 6 and 12 hours and Revusky (1968) and Rozin (1969) replicated and confirmed the effect.

> There were several hypothesis put forth to explain these results,
>
> Two early explanation, both using a mediated response position, were provided for these findings. First, some have suggested the possibility of stimulus after-effects which bridge the long delay from the mouth or stomach could served this function. One difficulty with this explanation is that a sucrose solution which is taken into the empty stomach is digested and absorbed into the blood stream in less than six hours, and yet it is possible to obtain an aversion to sucrose when the delay interval is this long.
>
> A related explanation has been that the organism vomits the consumed substance during toxicosis, so that the aversion may be produced by the continguity of vomited substances and the toxicosis. Such aversions are obtained, however, when there is nothing in the stomach to be vomited. Equally important, when rats are used as subjects, they do not have sphincture control that makes vomiting possible (Hall, 1976, p. 343).

Revusky and Garcia (1970) say that long delay learning can be explained in terms of the number of intervening, or interfering, stimuli. There are few potential CS's in taste aversion learning due

to the aspect of belongingness. Wilcoxon et al (1971), demonstrated that quail, using a visual CS, showed aversion learning even though a good many "extraneous" visual cues intervene in the 30-minute CS-UCS interval. This finding casts doubt on the theory that the ability to learn over long delays can be explained simply in terms of stimulus absence or interference.

"Learned Safety"

"In the absence of unfavorable gastro-intestinal events, as time passes following consumption of a novel solution, the animal learns that the solution is safe" (Scott & Quint, 1946, p. 477). This is Kalat and Rozin's learned safety theory (Best, 1975; Kalat & Rozin, 1973; Rozin & Kalat, 1971). As has been mentioned, rats do show less aversion to familiar foods than to novel solutions (Revusky & Bedarf, 1967). There is a positive aspect that serves as a bridge between learned safety and specific hungers: Green and Garcia (1971) found that rats allowed access to a distinctive tasting solution during recovery from an illness would subsequently show an increased preference for the taste. The taste associated with "getting better" was endowed with medicinal properties and the animal preferred it after the pairings. This is a type of learned safety and is the analog of the situation in which one deficient diet is rejected while the enriched diet is preferred since the deficient diet was associated with illness and the rich diet associated with recovery from illness (Zahorik & Maier, 1969). Usually, "learned safety" is spoken of in reference to learning that a food will not produce illness but the same mechanism is probably used to learn that a food, or a taste, is associated with

something even better than just non-illness, that is, recovery from illness. Such a mechanism lies at the heart of specific hunger theories.

It has been shown that minimum pre-exposure to a novel food leads to weaker aversion to that food than if totally new. The concept of learned safety, however, does not really explain why the long delay in learning is possible.

Preparedness vs. Equipotentiality

Nowhere is this topic better explained than by Seligman (1972, 1970). The abstract from his 1970 article:

> That all events are equally associable and obey common laws is a central assumption of general-process learning theory. A continuum of preparedness is defined which holds that organisms are prepared to associate certain events, unprepared for some, and contraprepared for others. A review of data from the traditional learning paradigms shows that the assumption of equivalent associability is false; in classical conditioning, rats are prepared to associate tastes with illness even over very long delays of reinforcement, but are contraprepared to associate tastes with footshock. In instrumental training, pigeons acquire key pecking in the absence of a contingency between pecking and grain (prepared), while cats, on the other hand, have trouble learning to lick themselves to escape, and dogs do not yawn for food (contraprepared). In discrimination, dogs are contraprepared to learn that different locations of discriminative stimuli control directional responding. In avoidance, responses from the natural defensive repertoire are prepared for avoidance shock, while those from the appetitive are contraprepared. Language acquisition and functional autonomy of motives are also viewed using the preparedness continuum. Finally, it is speculated that the laws of learning themselves may vary with the preparedness of the organism for the association and that different physiological and cognitive mechanisms may covary with the dimension (Seligman, 1970, p. 406).

Taste aversion studies have given much credibility and impetus to this theory of preparedness and similar theories of belongingness and stimulus relevance mentioned above.

One of the interesting logical conclusions derived from this theory is one that sheds doubt on the reasoning behind assuming that principles of learning discovered in animals can automatically be generalized to man. European ethologists, in contrast to American experimental psychologists always thought the behavior of an animal in its natural setting was related to its sensory capacity and to its response capability. Ethologists, therefore, never considered learning as a general process, but rather believed it to be a more specific process interacting with the animal's adaptive characteristics in order to enable each species to survive in its particular environment (Hall, 1976). Tinbergen (1951) wrote,

> The student of innate behavior, accustomed to studying a number of different species and the entire behavior pattern, is repeatedly confronted with the fact that an animal may learn some things much more readily than others... In other words, there seem to be more or less strictly localized 'dispositions to learn'. Different species are predisposed to learn different parts of the pattern. So far as we know, these differences between species have adaptive significance (Tinbergen, 1951, p. 145).

Many American investigators have also come to question the generality of learning, e.g., Breland and Breland (1966), Bolles (1970), Lockard (1971), Rozin and Kalate (1971), Seligman (1972, 1970), and Warren (1972). Quoting from Warren:

> ... behavioral observations indicate that the learning abilities of animals are specialized and as closely related to ecological factors as their sensory capacities are. Every species appears to have its own set of special learning abilities, each one evolved to facilitate adaptation to specific ecological and social requirements. Animals are now seen as 'intelligent' in distinctively different ways that are often more highly correlated with ecological than phyletic variables. Rhesus monkeys, for example, surpass cats and dolphins in the formation of visual discrimination learning sets, but are markedly inferior to dolphins in learning to emit vocal operants. Dolphins find their way about by echolocation, frequently under conditions of

> extremely limited visibility; their performance relative to monkeys on vocalization and visual discrimination tasks appears to reflect the importance of these processes in adaptation to their normal environment (Warren, 1972, p. 582).

Rozin and Kalat (1971) feel these differences make sense in terms of evolutionary adaptation. Hall states,

> An understanding of the role of learning and memory in food selection involves the discovery of specifically adapted learning mechanisms and the integration of these with genetically determined behavior patterns. Thus, these investigators conclude, there is no reason to assume that an extensive set of generally applicable laws of learning exist independent of the situation in which they are manifested (Hall, 1976).

Bolles (1970) proposed that animals are born with avoidance and defense reactions already part of their response repetoires. There are three forms of defense reactions: (1) running, or flying away, (2) freezing, or (3) aggression. Bolles contends that a gazelle does not run from a lion because it has been bitten by lions, but it runs from any approaching object because this response is innate, one of its "species specific defense reactions". Learning to avoid the lion by aversive consequences would have no survival value and would therefore be useless to the individual and the species. To survive, it must already have this running-away response and cannot afford to depend upon the environment to teach it.

Seligman (1972, 1970) uses taste aversion as the number one witness in presenting his case for "preparedness", most of which have been cited above (Garcia, Ervin, & Koelling, 1966; Garcia & Koelling, 1966; Garcia, McGowan, & Green, 1972; Revusky & Bedarf, 1967; Rozin, 1967; Rozin & Kalat, 1971; Zahorik & Maier, 1969). Briefly, Seligman maintains that any organism brings into a given experimental situation a specialized sensory and receptor apparatus with a long evolutionary

history. Any task the experimenter arbitrarily sets up for the organism to perform may be more, or less, suited to the animal. Put another way, the animal may be more or less prepared to learn any one arbitrary set of cues and consequences. There is a continuum of preparedness found in all organisms. Any particular organism may be prepared, unprepared or, contraprepared to associate certain events. He defines preparedness as the number of trials which must occur before learning occurred. All stimuli are not equally associable with any one conditioned response. All events are not equally associable, neither are stimuli, reinforcers or responses, as general process learning theorists maintain. Equipotentiality in terms of relating stimuli, responses and reinforcers is false and the continuum of preparedness an animal brings with him from his evolutionary past must be considered when theorizing about learning principles.

Seligman writes:

> Preparedness is more than an alternative to the equipotentiality premise, and it is more than just a name for an ease of learning continuum. We propose four general hypotheses which transform it into an effective theoretical tool with explanatory and predictive power: (1) Different laws of learning vary with the dimension of ease of conditionability. (2) Different physiological substrata vary with the dimension. (3) Different cognitive mechanisms vary with the dimension. (4) As the word "Preparedness" implies, the selective pressures exerted on a species determine where a contingency falls on the dimension (Seligman, 1972, p. 5).

This may seem a long way from taste aversion research, however, Seligman and many others use Garcia's work to support their statements. Some of the work of Tinbergen (1951) and Lorenz (1965) is also supported by the results of basic taste aversion research.

Period Five

Bitterman (1975) in Science doubts that the phenomenon of taste aversion is truly what proponents say it is, or that learning predispositions have been adequately demonstrated. At any rate, he claims there is really no evidence for associative predispositions. He points out that, since early research on taste aversion, shock has been conditioned to flavor, and Garcia admits this, but adds the delay of reinforcement possible in each case in much greater with illness and flavor. Bitterman brings up many old arguments that Garcia seems to have answered (Garcia, Hankins, & Rusiniak, 1976).

In Mitchell's reevaluation of some previously held notions about neophobia (Mitchell, 1976) he opposes Barnett's opinion that while wild rats are quite neophobic laboratory rats are not (Barnett, 1958), supposedly due to a degenerative process having occurred in laboratory rats as a result of domestication. In Mitchell's experiments all three strains, two laboratory and one wild, showed an initial avoidance to a novel container. "It was concluded that both wild and laboratory strains are neophobic and that strain difference are ones of degree, not kind" (Mitchell, 1976, p. 190).

One finding basic to Garcia's research and the preparedness concept is that conditioned aversions following radiation or drug-induced toxicosis are rapidly established if the conditioned stimulus is a distinctive flavor, but difficult or impossible if it is an exteroceptive stimulus, such as light or sound (Garcia & Kimeldorf, 1957; Garcia & Koelling, 1966; Garcia, McGowan, Ervin, & Koelling, 1969; Woods, Makous, & Hutton, 1969). Mitchell feels his results show

that given the appropriate circumstances, conditioning of an exteroceptive stimulus to the effects of toxicosis can occur. Wilcoxon et al, (1971) has shown this with quail subjects.

In 1976, in Science, Wallace published a nice summary of the puzzling aspects of taste aversion research. Her review covers all of the points discussed in this review.

In the area of applied research, Garcia and his fellow workers are doing studies in predator control problems (Brett et al, 1976; Ellins et al, 1977; Garcia, Hankins, & Rusiniak, 1976; Gustavson et al, 1976; Gustavson et al, 1974; Rusiniak et al, 1976). They have found that lacing sheep carcassas with lithium chloride, and then when ingested by coyotes, inhibits future sheep losses due to coyote predation.

Buresova and Bures (1977) have shown another interesting aspect, that general anesthesia imposed between CS and UCS does not change the acquisition or extinction of a conditioned taste aversion. Traditional Pavlovian theory maintains that the animal must remain alert for conditioning to occur.

CHAPTER III

METHODS

Preliminary Work

In previous work with other Oscars, a definite preference for live earth worms over chunks of beef heart was shown. The fish would not eat beef heart if there were earth worms available. When one group of Oscars was switched from live mosquito fish to live earthworms it required an average of 2.5 days for the fish to begin feeding. With beef heart, under similar circumstances, it required over six days for the Oscars to begin eating. Once accustomed to both foods they ate readily but always less beef heart, by weight, than worms. When changing from beef heart to worms for the first time, latencies were much less than when switching from worms to heart (24 hours compared to five days). With two groups, one raised on worms and the other beef heart, there is a very short latency (1 second) for either group to eat live mosquito fish when presented for the first time.

In a pilot study seven Red Oscars (Astronatus ocellatus) were fed live mosquito fish (Gambusia affinis affinis) from December 1972 until April 1973. At the time of the experiment they had been habituated to a 60 gallon tank and were fed at 7:00 a.m., at 12:00 noon and at 6:00 p.m. Overhead lights were on from 6:30 a.m. to 9:00 p.m.

At the beginning of the test period live earth worms were fed. It required the usual 2-3 days for all the Oscars to eat one or two worms per feeding. When they had all taken their first good sized

meal of worms, beef heart was substituted. After five days they ate readily. Then worms and heart were alternately fed for two days. They ate each quite well, although less heart.

After one of the worm meals, an overdose of Malachite Green (a common remedy for Ichthyophtirius, a skin protozoan parasite) was administered. Worms had been fed up until one hour before the first treatment. This overdose was repeated after their next meal, which was of worms, in 24 hours to insure illness. The fish exhibited illness by their lack of activity and heavy respiration. Worms offered between the first treatment and the second were not eaten but were "tasted", that is moved in the mouth, then spit out and left on the bottom, which demonstrated that the second treatment was probably unnecessary.

After the second treatment the water was completely changed (this had been done every week previously for five months) and they were allowed ten hours to recover. (Their activity and respiration had returned to normal within two hours after the fresh, de-chlorinated water was put in the tank). After ten hours they were offered worms again. The same "tasting" and spitting out occurred. To test for the presence of taste aversion conditioning, and to see if they were still sick and would not take anything, beef heart was given within seconds of their rejecting the worms. They ate it readily. For several days, thereafter beef heart was choosen when worms and heart were presented together. After a two week extinction (starvation) period the Oscars gradually began eating worms again.

Experiment I

Purpose. The purpose of Experiment I was to extend the study of bait shyness, or taste aversion, to a selected species of tropical

fish. The existance of taste aversion is of interest and an attempt will be made to demonstrate that existance and show that it is basically no different than in many other species.

Subjects and apparatus. Eight Jewel Fish (Hemichromis bimaculatus), averaging 22.5 grams, 10 centimeters long similar in size and coloration were obtained, when fry, at a local pet store and maintained for five months in individual five gallon tanks. They were all habituated to 76°F water, 50% of which was changed weekly. They were fed exclusively on shrimp pellets once a day at 9:30 a.m. The sides and backs of the four tanks were covered with paper so that they could only see out the front. Corner filters were used with locally purchased filter floss and charcoal. Lights were turned on at 8:00 a.m. and off at 5:00 p.m. A submersible, in-tank, 200 watt heater was used to maintain temperature. The same color gravel was used in all tanks.

Baseline data and definitions. During the five months of habituation, baseline data were collected mainly on three parameters, 1) amount consumed, 2) latency of approach to food, and 3) amount of "tasting". "Tasting" was defined as: when the fish took the food item in its mouth and fondled it, rolling it over and over, chomping on it, flashing minute pieces through its gills before either swallowing it or spitting it out. There were two measures used to record "tasting", 1) time spent with food in mouth and 2) the number of times the piece was spit out and taken up again. Approach latency was the time from the moment the food item hit the water surface until the food was taken into the mouth. The amount consumed was the weight of the food ingested per meal.

Baseline data, following habituation were consistent and predictable. On a 24 hour feeding schedule they always appeared hungry. They simply gulped their food with very short approach latencies (less than 1 second). "Tasting" of familiar, habituated and small food items was non-existant by definition. Tasting occurs of necessity, but is only coincidental as the food must pass through the mouth to get to the stomach. Fish simply gulp a familiar food when hungry. If consistantly fed as much as they'll eat the amount consumed slowly and progressively increases as their stomach capacity increases. With each successive meal their bellies act like progressively more inflatable bladders and a conspicuous bulge is visable. Over several weeks they have definite pouches which can hold a surprising amount of food. All fish were eating almost the same amount at the time of these experiments, about 1.5 grams (about 15 pellets) per meal. The pellets were .10 grams each. At meal time the fish stayed in the middle of the tank as close to the surface as they could get and waited for each successive pellet to drop. When they had had enough they went low to their usual spot by the filter.

In Experiment I, the fish should, 1) consume less, 2) show longer latencies of approach, and 3) the time period when "tasting" occurs should increase after illness is induced. With these three indices the phenomenon of taste aversion should be convincingly demonstrated. Extinction data, in terms of the above three parameters, was also recorded and analyzed.

Procedure. Following the five month habituation period treatment began. Each subject was fed the usual pellets, however, all had been rolled in ground deer meat (DB). This had proven to taste sufficiently

distinct in pilot studies. The pellet looks and feels the same, and is the same size, but tastes differently. The three parameters were recorded on the first encounter with this novel taste. Following this feeding six of the eight fish were made to vomit by the administration of .15 cc of Syrup of Epicac by intragastric tube. The control subjects were given the same amount of their own tank water by the same method. All eight were out of the water for about 15 seconds during this procedure. The Epicac was administered 30, 60, or 90 minutes respectively to the six experimental fish (2 each) after the DB flavored meal, and tank water 30 minutes after the DB flavored meal to the control fish. After the subject vomited and demonstrated signs of sickness, one half of the tank water was changed in order to collect all debris off the bottom. This procedure was usual for all fish since it was a weekly occurrence.

The next day at meal time the fish were fed their regular, habituated, unflavored pellet and behaviors were recorded. The following day (2 days post-treatment) the deer burger-flavored pellets were offered. Quantity consumed, latencies of approach and "tasting" data were recorded. The next day their regular, unflavored pellet was fed and on successive days was alternated with the DB-flavored pellet in order to observe extinction.

After each DB-feeding day's results were recorded, two pellets of regular-flavored diet was offered and readily eaten by all experimentals. Only the behavior relating to the DB-flavored pellets is recorded on those days, even though on those days, and immediately after DB data were recorded, some of their regular flavored diet was given.

Results. The results for the 30, 60 or 90 minute-delayed-illness differed very little and are combined in the figures. Upon first exposure to the DB-flavored pellets all three parameters documented the typical "new object reaction". After a normal first approach latency to the first pellet by the six experimentals, latencies were from two to five times normal (Figure 2). Amount of "tasting" increased both in mean time each food pellet was in the mouth (Figure 3) and mean number of times each piece was spit out and tried again, i.e. number of tasting trials (Figure 4). Mean quantity eaten decreased by 50% (Figure 5). Original data is shown in Table 1 in the Appendix.

These changes in behavior were not really as drastic as would be seen had an entirely different tasting food been used. The regular, long habituated pellet was still the base food and as a result of previous "learned safety" the fish ate many of the DB-tasting pellets due to familiarity with the underlying taste. That this was in fact the case was demonstrated by feeding straight deer-burger or a new, entirely different flavored pellet. On first exposure to entirely new foods in another pilot study, the fish ate much less and latencies were much longer and "tasting" continued until the pellets virtually fragmented, floating unconsumed. Using regular flavored pellets with just a coating of distinctive flavor somewhat tested their ability to discriminate. This procedure was equivalent to degrading the CS.

In the present experiment controls ate about the same amount as experimentals on day 0 (Figure 6). After illness and from the next day onward, differences were clear. The next day (day 1), since the experimental fish had essentially not eaten in 48 hours, they ate more of their regular, unflavored diet than controls, which had eaten,

Figure 2. Mean approach latencies to all food including seven baseline days. On day 0 novel food was introduced and toxic treatment followed at 30 (two Ss), 60 (two Ss), and 90 (two Ss) minutes. Two control subjects were treated with tank water 30 minutes after novel flavor. On day 1, and on every odd numbered day thereafter, all subjects received regular food. On day 2, and on every even numbered day thereafter, novel flavored (deerburger) pellets were offered in order to observe persistence and extinction. Taste aversion persisted in the experimentals until day 18.

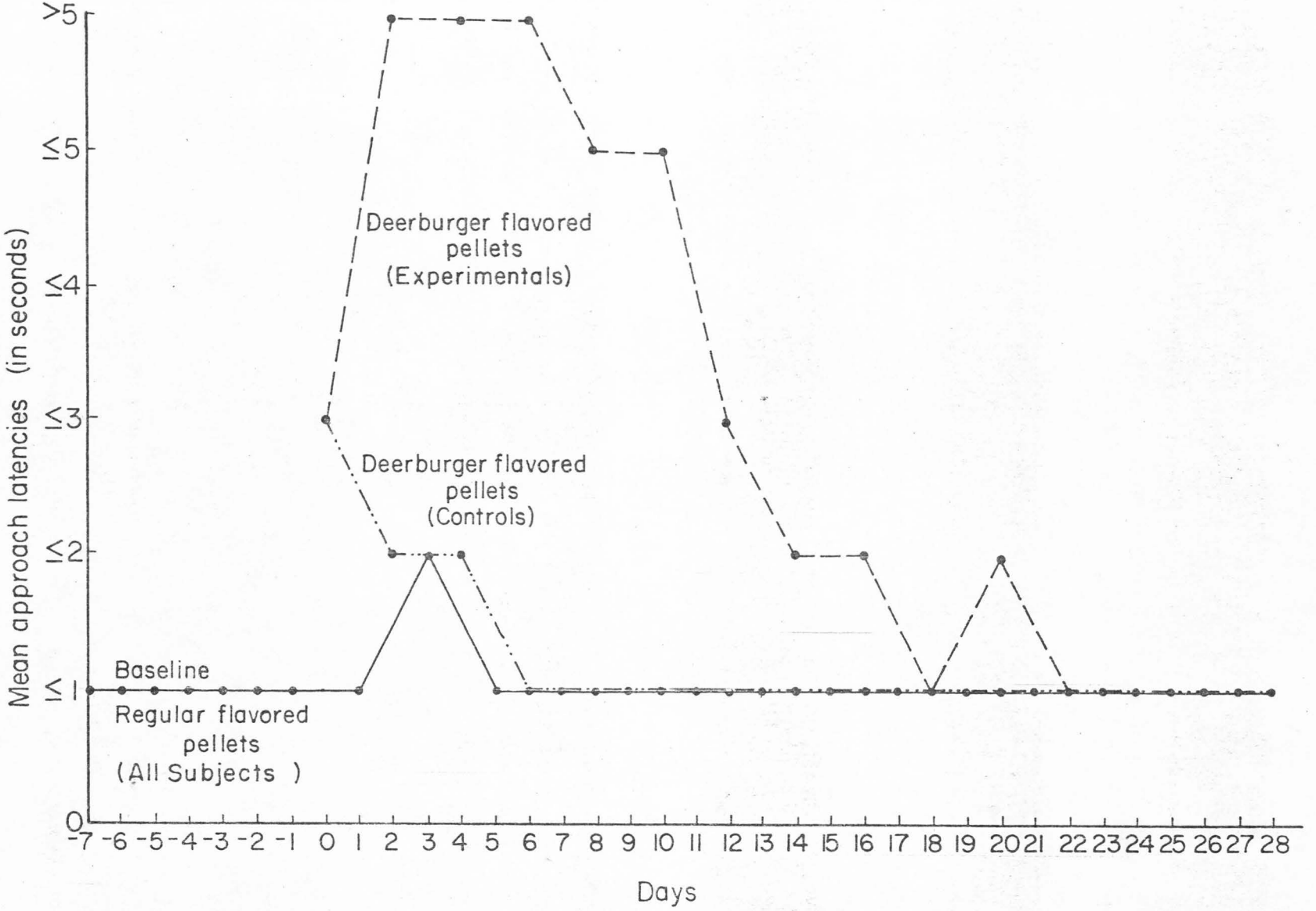

>5
≤5
≤4
≤3
≤2
≤1
0
Mean approach latencies (in seconds)
Deerburger flavored pellets (Experimentals)
Deerburger flavored pellets (Controls)
Baseline
Regular flavored pellets (All Subjects)
-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Days

Figure 3. Mean time that food was in the subjects mouth being tasted. Ten novel flavored (deerburger) pellets were offered on day 0. Illness was induced in pairs of subjects 30, 60, and 90 minutes later. Two control subjects received tank water 30 minutes after feeding on day 0. On day 1, and on every odd numbered day thereafter, all subjects received their regular food. On day 2, and on every even numbered day thereafter, deerburger pellets were offered.

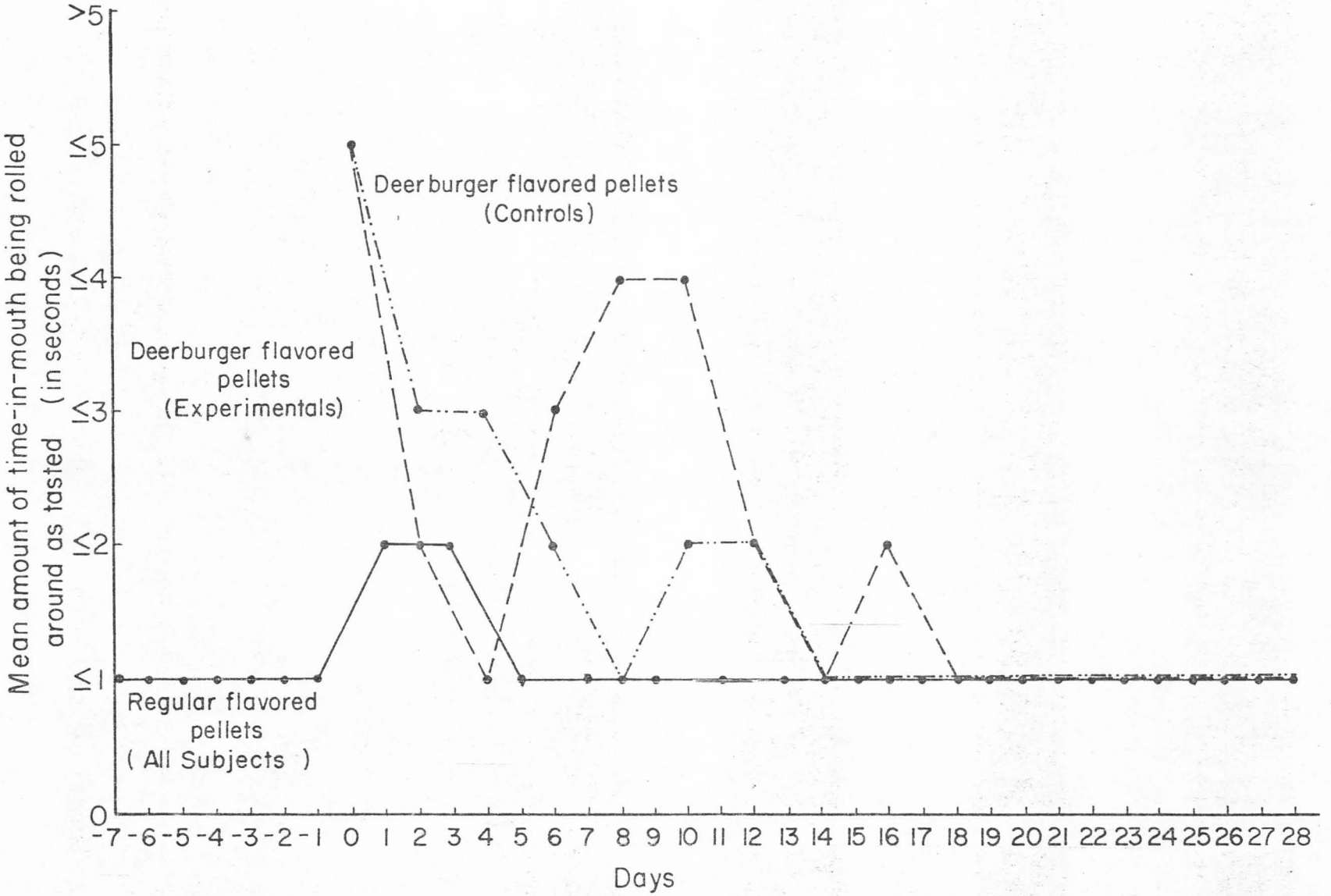

Mean amount of time-in-mouth being rolled around as tasted (in seconds)
>5
≤5
≤4
≤3
≤2
≤1
0
Deer burger flavored pellets (Controls)
Deerburger flavored pellets (Experimentals)
Regular flavored pellets (All Subjects)
-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Days

Figure 4. Mean number of times food pellets were taken in the subjects mouth and rejected. Days -7 to -1 are baseline days and contain no rejected pellets. On day 0 novel flavored pellets were provided and treatment followed 30, 60, or 90 minutes later. Control subjects lost all neophobic reactions by day 14. On every odd numbered day, beginning on day 1, regular food was offered. Deerburger was offered on even numbered days. Extinction of aversion was complete by day 18 for all six treatment subjects.

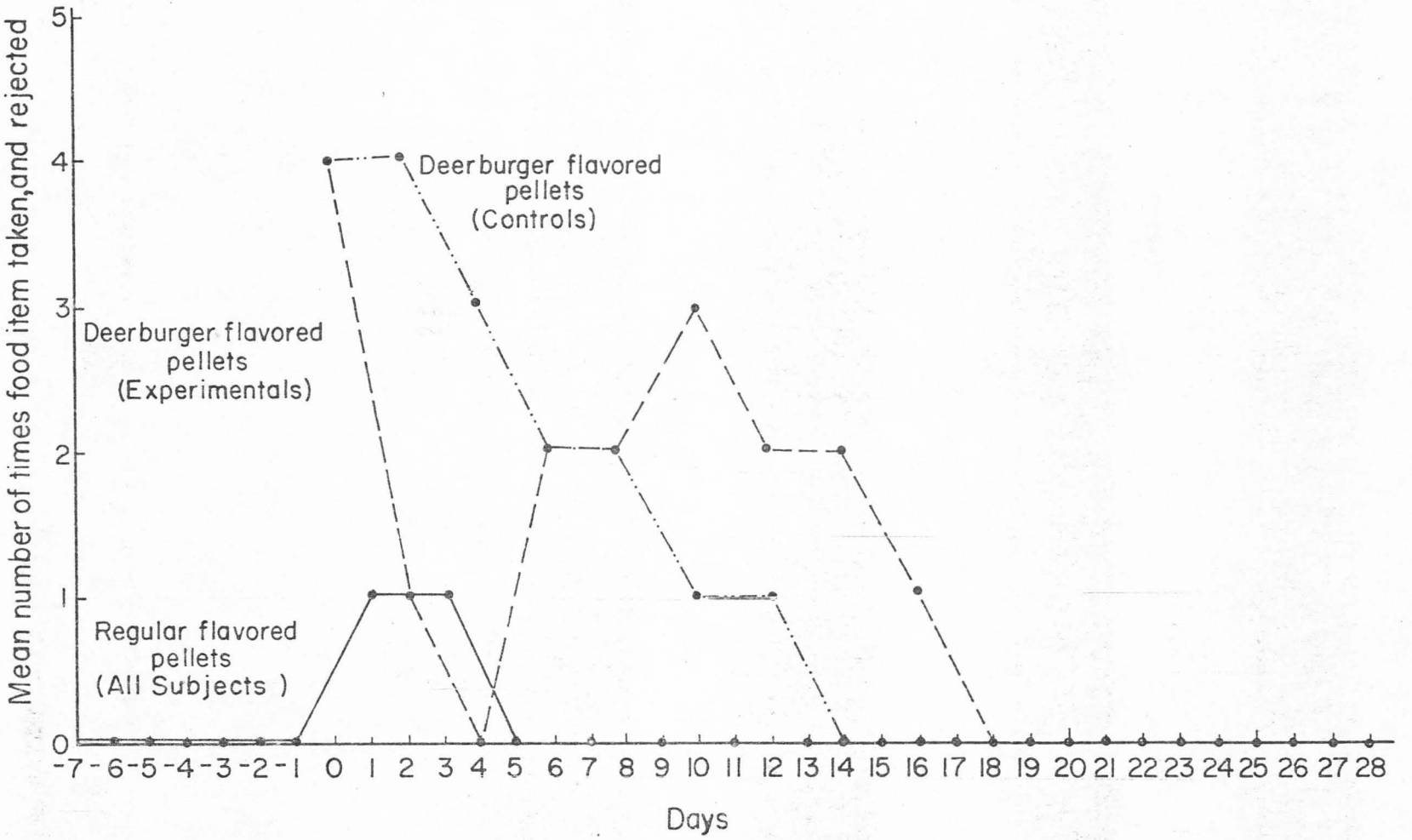

Mean number of times food item taken, and rejected
5
4
3
2
1
0
Deerburger flavored pellets (Controls)
Deerburger flavored pellets (Experimentals)
Regular flavored pellets (All Subjects)
-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Days

Figure 5. Mean weight of food consumed per day for all subjects combined in Experiment 2. Days -7 to -1 are baseline with only regular pellets offered. Illness was induced (30, 60, and 90 minutes) after the novel flavored pellets were fed on day 0. Deerburger and regular pellets were offered on alternate days from 0 through day 28.

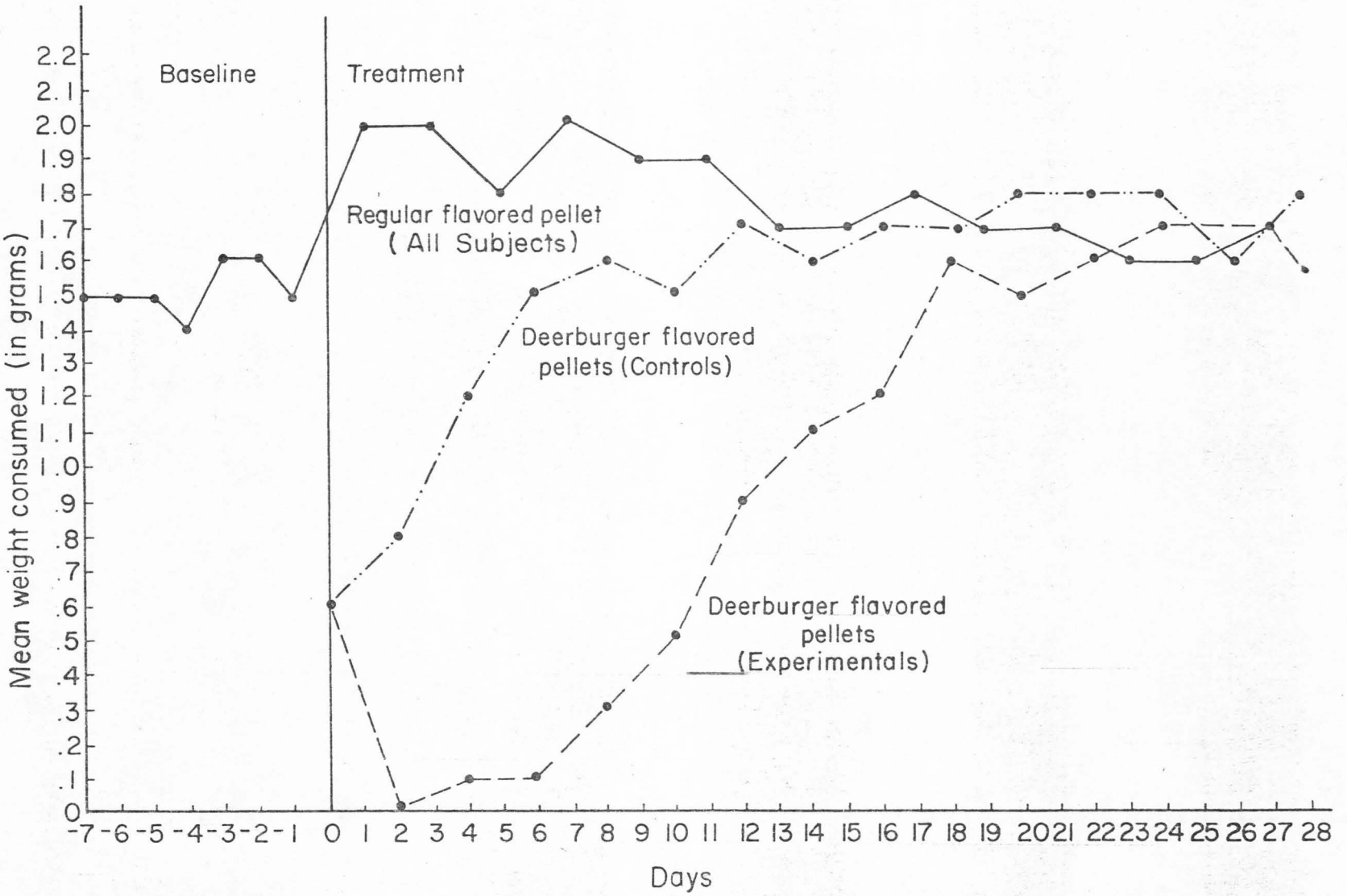
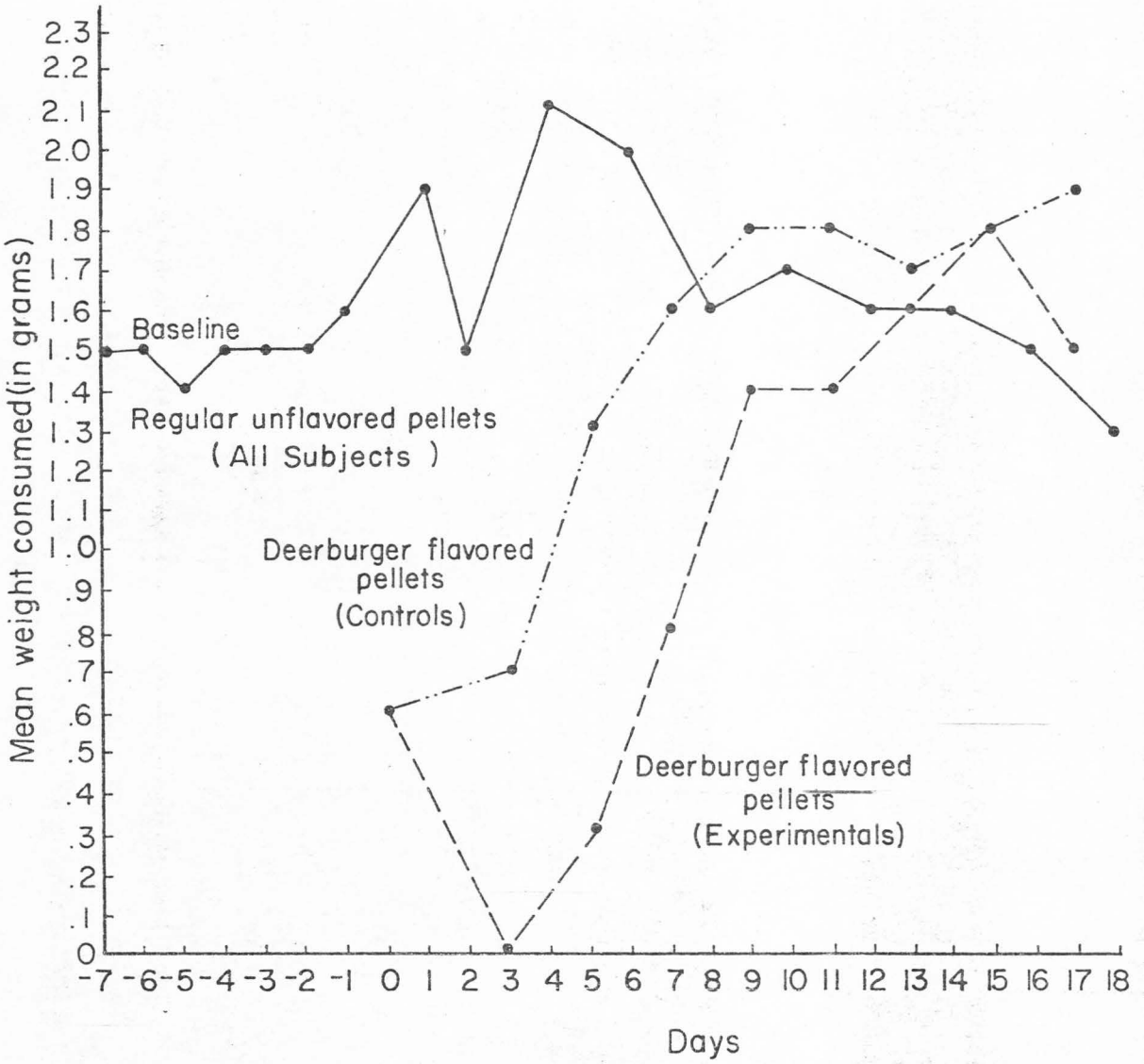

Baseline
Treatment
Regular flavored pellet
(All Subjects)
Deerburger flavored
pellets (Controls)
Deerburger flavored
pellets
(Experimentals)
Mean weight consumed (in grams)
Days
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28

Figure 6. Mean food by weight consumed by subject group in Experiment 2. Solid line represents combined experimental and control subjects' regular pellet consumption on odd numbered days (after day 0). Deerburger was fed on day 0. Treatment was administered after regular pellets on day 2. In spite of the 48 hour and two regular pellet feedings intervening between deerburger and treatment, all experimentals showed immediate and prolonged (at least 8 days).


Mean weight consumed(in grams)
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Days
Baseline
Regular unflavored pellets
(All Subjects)
Deerburger flavored
pellets
(Controls)
Deerburger flavored
pellets
(Experimentals)

and been allowed to digest the DB-flavored pellet. On the next day (day 2) DB-flavored pellets were offered all fish and the results were significant and obvious. Controls, having learned about the food by their previous single, unpunished exposure, ate more than the first time while the experimentals ate none. The experimentals would approach the first piece offered with the usual short latency, take it in their mouths, immediately spit it out and let it sink to the bottom. The second pellet was approached slower and spit out immediately. The third was approached only after it had almost sunk. The fish, after approaching it, would draw water through their mouths by gill action and "taste" it, or "smell" it, without taking it in their mouths. Ten DB-flavored pellets all on day 2 were offered and the fish only had to get close enough to pass water through their mouths that had passed over the pellets to not eat it. (With extinction, the fish gradually took more pellets in their mouths, pulverizing them and, swallowing more and more as trials continued alternating with days of regular, unflavored pellets). The next day's (day 3) meal was regular, unflavored pellets. The experimentals again ate more than baseline, since they had not eaten the day before, and more than the control which had eaten almost its usual amount.

Thereafter, feedings were alternated with unflavored and flavored pellets. It required 15 days before the treated fish ate a baseline amount of DB-flavored pellets.

It should be noted that on day two (the second day after being made ill) when DB-flavored pellets were offered, very little "tasting" occurred (Figure 3). It seemed to only take one "whiff" and they refused it. "Tasting" behavior did emerge on subsequent days (6, 8,

and 10), but decreased as familiarity precluded the necessity of "tasting" each flavored pellet.

These data should convey some notion of the obvious taste aversion behavior seen in this experiment. All the criterion for confirming taste aversion learning were more than adequately met. It is also notable that results did not significantly differ across the 30, 60, or 90 minute delays in illness in the experimental fish. Strong aversion was noted with a 90 minute delay.

Experiment II

Purpose. Experiment II was designed to demonstrate long delay learning, and food neophobia by showing that a fish could learn to associate a new food with being ill even though its regular, familiar diet was fed between the new food and the illness.

Subjects and apparatus. Apparatus was exactly as in Experiment I. Four naive Jewel Fish were used.

Procedure. The fish were habituated as before. The only difference between this experiment and Experiment I was to place one feeding of regular, unflavored pellets between the DB flavored pellet and the induced illness. On day 0, they were fed DB with no illness. They showed the normal initial reluctance to eat as in Experiment I. The next day (day 1) they were fed familiar pellets. Then in 30, 60 or 90 minutes three were made ill as before, one served as an untreated control. This procedure placed the normal, unflavored diet temporally much closer to the illness. On day two they were fed familiar unflavored pellets and changes in behavior recorded. On day three

DB-flavored pellets were offered and results recorded. Extinction data were collected as in Experiment I by alternating DB days with regular flavor days.

Results. The results were as expected (though weaker than Experiment I) since 24 hours and one feeding of regular diet intervened between the novel food and illness. Since there was probably no lingering trace of the DB-flavor present they could have only "remembered" and made the association over a phenomenally long period of time. On day three they refused the DB-flavored pellets and all subsequent data resembles that of Experiment I. The fish ate less, took longer to approach and, "tasted" longer when given the DB-flavored pellets. This behavior differed significantly from baseline before the illness and from that of controls. Amount of DB consumed is shown in Figure 6. Again, on days when DB-flavored pellets were offered and after behavior was recorded, regular diet was offered. They always ate it greedily. The difference between the 30, 60 or 90 minute illness delays was insignificant. Table 2 in the Appendix contains raw data.

This data further strengthens the findings of this thesis. There was obviously some "learned safety" involving the regular, habituated diet since the subjects behaved as if it could not have been the familiar food, as opposed to the new food they had eaten the day before, that made them sick. The control, after some initial reluctance, eventually ate more of the new diet than the old, as did the experimentals following two weeks of extinction. By day 20 (Figure 6) all were eating DB rapidly.

Experiment III

Purpose. Experiment III was designed to see if eteroceptive cues could effect eating as did taste cues. This experiment attempts to demonstrate whether or not a place, or position in the tank where the fish eats, can take on the effect of signaling future illness if something is eaten in those surroundings.

Subjects and apparatus. For the place aversion experiment taste was not the intended cue (CS) but "place" was. Individuals of five different species were made ill in one, distinctively decorated, end of individual 20 gallon, 30 inch "long" tanks. The food was always the same in both ends for each particular fish, but different fish got different foods. Illness was induced (as in Experiments I and II) after ingesting a meal in the designated tank end 30 minutes after that meal. There were screen dividers to confine the fish in the appropriate end for feeding, treatment and, illness. They were fed the same food in the other end of the tank but never made ill in that end. All the foods used for this study were fed to the fish after they had habituated to the routine for four weeks. This means that the foods were not completely novel but were more so than the regular diet.

The two ends of these relatively long tanks were backed with either different colored paper, different patterns, or different colored lights.

Three Jewel Fish (Hemichromis bimaculatus), a single Tilapia mosambique, one Green Sunfish (Lepomis cyanellus), one Convict (Cichlasoma nigrofasciatum), and one Black Bullhead (Ictalurus melas), were housed individually in tanks and habituated four weeks with color and pattern end differences. Two of the Jewel Fish were used

as controls. The seven different foods used were, DB-flavored pellets, Tetramin Flakes, freeze dried brine shrimp, freeze dried squid, freeze dried tubifex worms, "Long Life" flakes, and Tetramin pellets. At the start of the experiment all fish were eating their respective foods well and maintaining body weight and/or growing.

Procedure. On day 1 all fish were fed in the left (south) end of their tanks. All were made ill with Syrup of Epicac except the two controls which received an equivalent amount of their own tank water. Vomiting was observed as were other typical signs of illness. All were treated 30 minutes after eating. Three hours later the tank water was replaced with seasoned, fresh water and the divider removed. Signs of illness never lasted more than 30 minutes after this water change.

The following day all were fed the same food in the right (north) end of their tanks where they were confined by the divider. Thirty minutes after eating they were caught as before but were given their own tank water by intragastric tube. This treatment caused no signs of illness. After three hours the tank water was changed as before and they were allowed access to the entire tank. This procedure continued every day for two weeks, ill in the left end after a meal and not in the right.

If "place" (tank end) had taken on discriminative stimulus properties, food consumption should have decreased in the end they were made ill in on the test day and increased in the opposite end. Since food consumption did not decrease differentially treatment sessions continued over two weeks.

Results. Controls, became accustomed to this handling within a few days and amount of food consumed did not decrease or increase in

either end, as expected. They maintained weight, and seemed to make no association between food, place, handling, or intragastric ingestion of tank water.

The five experimentals were a different story. Even as soon as the next meal following their first illness, quantity of food consumed dropped off. They did not increase food consumption in the "safe" end but in fact decreased food intake in both ends. After two weeks they had lost weight and by their economy of movement it was obvious they did everything to conserve energy. They had developed an aversion to food but not the particular end of the tank, even though they were never ill in one end but only made ill after a meal in the left end (every meal they had in the left end, i.e., every other day's meal).

If the CS had been a potential prey item the fish may have attacked (tasted) it in a form of territorial defense and hence shown place conditioning. Results were the same whether colors, patterns, or green and white lights. "Place" did not become associated with the illness. If they had been shocked in one end and not the other, "place" would have signaled shock and would be avoided. Such "place" avoidance has been demonstrated in many shuttle-box conditioning experiments (Wodinsky et al, 1962).

CHAPTER IV

DISCUSSION

It appears that fish acquire aversion to tastes in much the same way as rats. If there is a contimuum of learning which places fish lower than rats, it was not demonstrated by the present results. Fish learn to avoid tastes which have been associated with aversive consequences just as readily as rats. At present there is no truly objective way to prove that these experiments are exactly analogous to those with rats or that there are absolutely no confounding stimuli or consequences. Nevertheless, these experiments appear analogous and the conclusion can be made that taste aversion does exist in fish. In terms of the first objective of this thesis, the phenomenon of conditioned taste aversion, as it exists in experiments with fish, looks similar in every respect to original and classic work with rats.

Neophobia, in the form familiar to those studying rat feeding behavior for years, appears to be present in the same form and controlled by the same parameters in fish. Even though Experiment II did not use more than one familiar food in contrast with a novel food, the phenomenon was still very apparent. The 48 hours between the new taste and illness is the longest CS-UCS interval in all the relevant literature. If researchers could identify the mechanism by which that gap is bridged much of that which is unknown and controversial concerning conditioned taste aversions might be explained. This writer feels we do not give evolution enough credit in that, when dealing with an aspect of behavior like feeding, the animal has had to develop ways to associate tastes and nausea, or improving from illness, over

long delays in order to survive. There are many forms of food poisoning where the bacteria causing the illness need time to induce malaise. That period of time in some cases is 18 hours or more. Those animals which could make that long an association have survived and those that could not have died. Knowing something about how the phenomenon came about and how it is maintained does not always help in explaining what mechanisms are operating at the present time. This demonstrates the existence of neophobia but, an even more interesting question is how the UCS-CS gap is bridged, and what are the cues and consequences associated within the underlying physiological mechanisms.

It is puzzling that animals learn positions in space with minimal exteroceptive punishment when the response-consequence interval is very brief. It has been demonstrated that rats can use taste cues to avoid foods but not to avoid places, and that peripheral pain can easily be associated with location but not with taste. The separation of connectable stimuli is the same for fish as shown in this thesis. If illness had been induced immediately upon the subject's entering a compartment then the compartment itself might more readily have become a cue to forthcoming aversive consequences. When the delay between CS and UCS is long however, as is "inherent" in the feeding system of the animal, places, or location, and all peripheral cues probably diminish in their ability to signal that illness is imminent. It is probably the case that the longer an animal is in a particular compartment, which is later associated with illness but prior to illness, the weaker the association is to the compartment and the stronger the association is to any flavor.

Experiment III supports the "stimulus relevance" principle which maintains that "the associative strength of a cue with some consequence depends, in part, on the nature of the consequence" (Revusky & Garcia, 1970). And, as Green, Bouzas and Rachlin (1972) put it, "These results lend support to a view of adaptive specializations in learning wherein the effectiveness of a cue is restricted by the nature of its consequences." Garcia, McGowan and Green (1972) have also demonstrated substantial differences between the effects of illness and electric shock on a rat's drinking behavior. They suggest there exists a neurological center where taste is associated with visceral but not with peripheral cues. In short, "place", a peripherally important stimulus, has no natural reason to be associated with something going on in the milieu interne and, therefore, consequences of visceral importance are not naturally associated by the animal to information about the milieu externe.

As for contributing to the accumulating evidence for the "belongingness" and "stimulus relevance" principles, as well as the argument that the laws of learning may not be the same for all animals, the present findings are clear. Some animals, through evolutionary selection (to "fit" their particular environment), are more inclined to one sort of action in certain circumstances than another and taste aversion studies show this. The stimulus-response connections are such that appropriate associations are made easier than unappropriate ones. As with pigeons, and the difficulty one has in teaching them to defend themselves aggressively instead of flying away, it is obvious that evolution has selected some neural connections over others just as it has selected limb-type and eye size. (Anatomy and physiology are too, a function of their consequences). Those associations more easily

made than others are those which must be made quickly and without mistake in order for the animal to survive and make sense of its environment. It makes no sense and has no survival value for example, for a rat to associate walking with the nausea and vomiting caused by a new food ingested two hours previous. The rat must associate the illness with the food (flavor) or it would make the same mistake again, and it is only those rats that can make such an association that have survived and passed on this ability. The association, and the correct one at that, was made even though the illness came on as it was walking back to its nest. The fact that the rat did not associate the illness with walking or other exteroceptive environmental stimuli, temporally much closer to the illness, is compelling enough to seriously question the equipotentiality premise. That animals learn some things more easily than others is obvious.

All behavior is underscored by anatomy and physiology which is the product of natural selection within the evolutionary process. It follows that those anatomical and physiological constraints are inherited and, therefore provide underlying boundaries on behavior. Survival has always been contingent upon certain kinds of behavior.

It is true that many responses are strengthened by their consequences. When a hungry organisms' behavior produces food, that behavior is reinforced and is therefore likely to recur. The premise that behaviors, attempted for the first time, such as food getting or warmth seeking, are randomly emitted is not acceptable. When an animal is hungry for the first time it is more likely to emit an already selected and narrow set of responses, a set which is "naturally" more likely to result in reinforcing consequences, than the broad

range possible in it's repertoire. That is why puppies, minutes after birth, struggle in a particular way, emitting a very narrow set of responses which are most likely to be reinforced by milk, than any one or several other possible responses. These narrow sets of behavior are relevant to the situation, or deprivation: they are not random. If the first time a baboon saw a lion it picked up a nut to eat, it would be dead. The fact is that the baboon has a narrow set of responses to emit relevant to the situation. With experience the baboon becomes more efficient through modification and refinement in his escape but the initial neophobia was ready made. Animals are prepared to emit certain responses rather than others. A narrow set of appropriate responses can be emitted in a given situation without the help of prior experience. From then on however, the environment sharpens the set even further and modifies that response class so it becomes very efficient.

Skinner (1974) in discussing the phenomenon of imprinting, states that a duckling does not inherit the behavior of following a moving object but, "What the duckling inherits is the capacity to be reinforced by maintaining or reducing the distance between itself and a moving object". The difference in the two is that one is refineable by environmental experience. The "raw response" was genetically programed to occur given circumstances appropriate to it. All animals do certain things that are obviously appropriate to the situation when they could not have had the chance previously to learn which was correct. That they can be taught other behaviors is clear but the range of difficulty indicates an innate preparedness. What this shows is that behavior is adaptable, and needs to be, so that if ever

contingencies are such that mating is an appropriate response in the face of a predator that such is possible. Survival of a species might occur because one mutant got it's behavior sets mixed and mated instead of ran. That many species have apparently not been able to learn contraprepared behaviors is perhaps demonstrated by the number of extinct species. The behavior sets they had to cope with were too narrow and inflexible. Luckily, natural laws are not random, either, and animals do have some security with genetically influenced behavior and some confidence that nature does not usually trick them. It is as if ancestoral animals, in preserving their own lives, did it all to aid their descendants in an effort to predict the consequences of an environment that might kill. The roots of behavior order the many possible reinforcers in the environment to make sense. "Making sense" in this context means having survival value.

There is not a "tabula rasa," and responses, prior to reinforcement by environmental consequences, are not randomly emitted. There are narrow sets of specific responses emitted appropriate to the situation upon which environmental consequences effect their influence for refinement.

Since illness may be brought about by many factors completely unrelated to any particular food ingested, care must be taken in fish hatcheries so as not to inadvertently establish a taste aversion situation with food that might later be used as bait by fishermen.

Tropical fish producers often have trouble with parent fish eating their young. This is usually solved by separating the young from the parents and is generally a satisfactory method. Many home hobbyists like to keep the young with the parents, however. Taste

aversion is a means by which parents may be taught an aversion to the taste of their own young and therefore they may co-habitate peacefully. Some fish, however, do not have adequate musculature for emesis, e.g., Angel Fish (Pterophyllum) and Discuss (Symphysodom), and therefore, an illness inducing agent must be administered with care. The active alkaloid (Emetine) in syrup of Epicac is acutely toxic to the heart, liver and kidney if sufficient amounts are absorbed.

Taste aversion also has application in predator control, specifically with the coyote-sheep problem. Garcia (Gustavson et al, 1974) have recorded decreases in sheep loss after treatment, but exactly to what the decreases might be due is controversial. That the principle works in laboratory situations is true but it is also true that this is a long step from stopping significant sheep and lamb losses on the range.

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APPENDIX

Table 1. Mean weight consumed (in grams at .1 gram per pellet) for experimental (1-6) and control (7-8) subjects across 34 days in Experiment 1. These figures correspond to points on Figure 5. Regular (R) diet was fed for the first 5 days then alternated with deerburger (DB).

Subject	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9
(Exp.) 1	1.5	1.5	1.4	1.6	1.6	.6	2.1	0	2.2	0	2.5	.1	2.3	.2	2.1
(Exp.) 2	1.5	1.3	1.5	1.6	1.5	.4	1.8	0	2.2	0	2.4	0	2.4	.1	2.0
(Exp.) 3	1.7	1.6	1.8	1.8	1.7	.6	2.0	0	2.1	.1	1.9	.1	2.0	.3	2.1
(Exp.) 4	1.4	1.3	1.6	1.3	1.4	.6	2.3	0	2.2	.1	1.8	.1	1.7	.3	1.9
(Exp.) 5	1.4	1.5	1.5	1.7	1.6	.4	2.2	0	2.3	0	2.3	.1	2.5	.4	1.8
(Exp.) 6	1.5	1.4	1.6	1.8	1.6	.8	1.9	0	2.0	.2	1.4	.1	2.0	.4	1.9
(Cont.) 7	1.5	1.3	1.5	1.5	1.3	.5	2.0	.7	1.7	1.2	1.1	1.4	1.5	1.5	1.7
(Cont.) 8	1.5	1.4	1.7	1.6	1.4	.8	1.9	.8	1.6	1.2	1.2	1.5	1.5	1.7	1.7
Diet	R	R	R	R	R	DB	R	DB	R	DR	R	DR	R	DB	R
DB Exp $\bar{x}$						.56		0		.1		.1		.3	
DB Cont $\bar{x}$						.65		.8		1.2		1.5		1.6	
R-Both $\bar{x}$	1.5	1.4	1.6	1.5	1.5		2.0		2.0		1.8		2.0		1.9

10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
.3	1.7	.8	1.8	1.0	1.6	1.0	2.0	1.7	1.6	1.4	1.6	1.5	1.7	1.7	1.6	1.7	1.5	1.6
.4	2.3	1.0	1.8	1.2	1.5	1.5	1.8	1.8	1.7	1.5	1.7	1.6	1.8	1.6	1.6	1.7	1.7	1.6
.7	1.9	1.3	1.7	1.2	1.5	1.3	1.8	1.5	1.8	1.7	1.7	1.7	1.4	1.9	1.7	1.8	1.8	1.6
.8	1.8	.9	1.7	1.1	1.9	1.2	2.0	1.5	1.7	1.4	1.8	1.5	1.6	1.6	1.5	1.5	1.5	1.8
.5	2.1	.7	2.0	.9	2.0	1.2	2.1	1.4	1.7	1.3	1.5	1.7	1.5	1.7	1.5	1.7	2.0	1.5
.5	1.8	.8	1.7	.9	1.7	1.1	2.0	1.6	1.6	1.5	1.7	1.4	1.5	1.6	1.8	1.6	1.7	1.7
1.4	1.8	1.7	1.6	1.5	1.8	1.7	1.5	1.6	1.7	1.7	1.6	1.8	1.6	1.7	1.7	1.5	1.6	1.8
1.5	1.7	1.7	1.5	1.6	1.7	1.7	1.4	1.8	1.7	1.8	1.9	1.8	1.7	1.9	1.6	1.6	1.6	1.8
DB	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB
.5		.9		1.1		1.2		1.6		1.5		1.6		1.7		1.7		1.6
1.5		1.7		1.6		1.7		1.7		1.8		1.8		1.8		1.6		1.8
	1.9		1.7		1.7		1.8		1.7		1.7		1.6		1.6		1.7	

Table 2. Mean weight consumed (in grams at .1 gram per pellet) for 3 experimental (Exp.) fish and 1 control (Cont.) across 24 days. Numbers correspond to points on Figure 6 for Experiment II. Means are shown combined for Exp. and Cont. subjects (R-Both) as well as separately for each group.

Fish	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
(Exp.) 1	1.5	1.5	1.4	1.5	1.5	.5	2.0	1.4	0	2.3	.1	2.1	.8	1.6	1.2	1.6	1.2	1.5	1.6	1.6	1.9	1.8	1.5	1.2
(Exp.) 2	1.4	1.5	1.5	1.5	1.7	.6	2.0	1.5	0	2.1	.4	2.1	.8	1.5	1.5	1.7	1.4	1.8	1.6	1.6	1.8	1.4	1.6	1.2
(Exp.) 3	1.5	1.4	1.5	1.4	1.5	.6	1.9	1.5	0	2.2	.3	2.0	.9	1.7	1.5	1.7	1.7	1.5	1.5	1.5	1.8	1.4	1.5	1.3
(Cont.) 4	1.3	1.5	1.5	1.5	1.6	.6	1.7	1.5	.7	1.7	1.3	1.8	1.6	1.5	1.8	1.7	1.8	1.6	1.7	1.6	1.8	1.6	1.9	1.6
	R	R	R	R	R	DB	R	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB	R	DB	R
DB Exp $\bar{x}$						.6			0		.3		.8		1.4		1.4		1.6		1.8		1.5	
DB Cont $\bar{x}$						.6			.7		1.3		1.6		1.8		1.8		1.7		1.8		1.9	
R-Both $\bar{x}$	1.4	1.5	1.5	1.5	1.6		1.9	1.5		2.1		2.0		1.6		1.7		1.6		1.6		1.5		1.3