CONDITIONED TASTE AVERSION IN SELECTIVELY BRED RAT STRAINS*

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A B S T R A C T

Development of conditioned taste aversion was investigated in five strains of rats. The Roman low-avoidance conditioning (RLA/Lu) and the Maudsely reactive (MR/Har/Lu) strains learned taste aversion faster than the Roman high-avoidance conditioning (RHA/Lu) and Maudsely nonreactive (MNR/Har/Lu) strains respectively. The low-avoidance strain displayed the highest magnitude of taste aversion learning and the non-reactive strain showed the lowest amount of learning. The control strain (RCA/Lu) was intermediate between the high-avoidance and low-avoidance strains in the magnitude of taste aversion learning. Some of the various mechanisms or components of taste aversion learning (that is, taste preference, amount of CS consumed prior to conditioning, and sensitivity to the UCS) which could possibly account for the genetic differences in taste aversion learning were investigated. It appears that the genetic differences in taste aversion learning rates of the MNR/Har/Lu, MR/Har/Lu, RHA/Lu, RLA/Lu and RCA/Lu are not due to differences in taste preference or the amount of CS consumed. There was no direct relationship among the five strains between the magnitude of taste aversion learning and sensitivity to the UCS. This investigation also found no evidence to support a classical conditioning model of taste aversion learning.

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When an animal suffers toxicosis contingent upon ingestion of a distinctively flavoured substance, the animal will readily learn to reject that substance upon subsequent exposures to it. (Garcia, Kimeldorf, and Hunt, 1961; Garcia and Koelling, 1967: Smith and Birkle, 1966). This phenomenon is called conditioned taste aversion and over the past few years it has been a subject of much research. Typically a taste aversion is established by allowing the animal to consume a flavoured substance (CS) and then later subjecting the animal to toxic aftereffects (UCS) produced by the injection of poison or exposure to X-irradiation.

FACTORS CONTROLLING TASTE AVERSION LEARNING

The variation in the intensity of learned aversions are a function of at least four main factors: a) the time interval between ingestion and poisoning; b) a number of properties of the CS (for example, stimulus relevance, novelty, salience and, the amount of the CS consumed); c) the strength of the UCS; and d) the nature of the thirst stimulus. A brief discussion follows concerning each of these factors.

Interval Between the CS and UCS

The conditions under which taste aversion learning occurs seem different from those under which traditional operant and classical conditioning ordinarily occurs. This type of learning can occur after a single pairing even when the toxicosis follows the ingestion of the substance by several hours (Revusky, 1968; Smith and Roll, 1967). This conflicts with

the traditional belief that effective learning does not occur if a response is temporarily separated from its consequences by over a few seconds or so.

The magnitude of the taste aversion declines as the interval between ingestion and poisoning increases. Wright, Foshee, and McCleary (1971) found a significant effect for injection delays of 30 minutes, 75 minutes, and 120 minutes. Kalat and Rozin (1971) also report that increases in the delay of poisoning (from ½ hour to 24 hours) cause decreases in learned aversions to a test solution.

Properties of the CS:

(a) Stimulus Relevance

Another traditional assumption is that any stimulus which serves as a CS is as readily associated with one consequence as another. Studies in taste aversion learning have shown that chemical stimuli (gustatory, olfactory) have a high associative strength relative to the consequence of toxicosis while telereceptive stimuli (auditory, visual) have a low associated strength. When the consequence is peripheral pain the converse is true.

For example, an animal will avoid eating a distinctly flavoured food if it has been followed by illness but not the place where the food was eaten (Barnett, 1963). However, if in the same situation electric shock is applied to the paws the animal will quickly learn to avoid the place in which it was painfully stimulated.

Another example is that rats will maintain or increase their consumption of distinctively flavoured food previously paired with electrocutaneous shock, but will markedly decrease their consumption if this flavour has been paired with illness induced by injections or x-rays (Garcia, McGowan and Green, 1972; Green, Bouzas and Rachlin, 1972). When flavour is held constant, rats will hesitate to approach a visually distinctive food that has been previously paired with shock, but will approach and eat this food readily if it has been followed by illness (Garcia and Koelling, 1966; Garcia, McGowan, Ervin, and Koelling, 1968). However, this readily made association appears to be species-specific. For the quail, visual aspects of the food are more important in learned aversion than its taste (Capretta, 1961; Wicoxon, Dragoin, and Kral, 1968).

It appears that some chemical stimuli have a higher associative strength relative to the consequence of toxicosis than other chemical stimuli. For example, smells are intermediate between telereceptive stimuli and flavours in their associative properties (Garcia and Koelling, 1967).

Green and Rachlin (1973) found that rats developed a strong aversion to a specific flavour paired with rotation. In this respect, the aversive properties of rotation are similar to the aversive properties of illness-producing agents, such as chemical toxins or x-irradition, and are different from the aversive properties of electric shock.

Associations can occur in the absence of stimulus relevance but such associations can be obtained only after prolonged training and the magnitude of the effect is not as large as is usually

obtained when relevant stimuli are available (Andrews and Cameron, 1960; Coppock and Chambers, 1954; Goldberg and Schuster, 1967; Miller and Kessen, 1952; Teitelbaum and Epstein, 1962). For example, Garcia, Kovner, and Green (1970) found that rats can learn to use the flavour cue to avoid shock. This learning took place after 20 to 28 trials, a performance that is much slower than taste aversion learning but compares favourably with shuttlebox avoidance when visual or auditory cues are used.

It seems that some special learning mechanism may have evolved which allows certain consequences to be more easily associated with their probable cause than with irrelevant stimuli (Garcia and Ervin, 1968; Revusky and Garcia, 1970). Seligman (1970) explains that organisms are prepared to associate certain events, unprepared for some, and contraprepared for others. Examples of this can be found in both classical (Garcia and Koelling, 1966; Rozin, 1967, 1968) and instrumental learning (Thorndike, 1964; Konorski, 1967; Rachlin and Hineline, 1967; Brown and Jenkins, 1968).

(b) Novel vs. Familiar Stimuli:

Rats are likely to consume a number of substances prior to toxicosis. How then can they detect which of the substances actually produce the toxicosis? Avoidance of all the substances would hardly be an ideal solution because the rats would starve to death. The logical solution would be for the rat not to associate familiar, relevant stimuli with a toxicosis, if novel, relevant stimuli are present. For if the

familiar substances were poisonous, the rat would likely be already dead.

The evidence indicates that, in fact, aversions to flavours will be less pronounced if the flavours are familiar than if they are novel, thus habituation to a flavour reduces the associative strength of that flavour (Farley, McLaurin, Scarborough, and Rawlings, 1964; Fenwick, Mikulka, Klein, 1975; Garcia and Koelling, 1967; McLaurin, Farley and Scarborough, 1963; Revusky and Bedarf, 1967).

It should be mentioned that aversions to familiar flavours can be obtained quite readily if no other relevant stimulus is available (Garcia and Koelling, 1967). Thus novelty is not a necessary condition.

(c) Salience:

A number of studies have shown that there is greater aversion for a more preferred substance than for a less preferred (Green and Churchill, 1970; Sutker, 1971). However Kalat and Rozin (1970) found that there was greater taste aversion for the least preferred of four solutions and the second highest aversion was for the most preferred. The tendency of a novel solution to be associated with subsequent poisoning was termed by Kalat and Rozin as "Salience".

It is not certain what the basis for the salience effect is.

There are a number of determinants that could contribute to this phenomenon such as specific taste properties (chemical properties) and strength of stimulation (amount of afferent activity). In support of the strength of stimulation interpretation Dragoin (1971) found that rats showed stronger learned aversions to more concentrated HCL solutions.

Kalat (1974) proposed that rats form stronger aversions to solutions that are more novel than other solutions, rather than more concentrated, since the more concentrated solution is also ordinarily more novel. Kalat found that when rats are poisoned after drinking 2 concentrations of the same solute, rats reared on water acquire aversions mainly to the more concentrated solution, but rats reared on a still more concentrated solution acquire aversions mainly to the less concentrated solution, which for them is more novel.

(d) Amount of the CS Consumed:

Bond and DiGiusto (1975) and Bond and Harland (1975) demonstrated that the strength of a rat's aversion to saccharin is a direct function of the amount of saccharin it consumed prior to poisoning. A previous report by Smith and Morris (1963) found that the amount consumed had no effect on the magnitude of aversion. However, in this study maximal degrees of aversion may have been produced due to using the more sensitive two-bottle test with large values of x-radiation. Also, the range in amounts consumed (4.6-9.2g saccharin solution) may have been insufficient to produce differential results. It is apparent that special care

should be taken to control for the possible effects of the amount consumed in experiments on taste aversion learning.

Strength of the UCS:

The intensity of learned aversions increases as the strength of the poison increases. Nackman and Ashe (1973) obtained a dose response curve between various volumes of 0.15 M LiCl injected and the degree of aversion. When the LiCl concentration was varied inversely with the volume injected, it was found that the aversion was dependent on the absolute quantity of LiCl and not on the concentration or volume of the solution.

Other researchers have reported that the magnitude of an aversion to a flavour by toxicosis increases with the severity of the UCS (Garcia, Ervin, and Koelling, 1967; Revusky, 1968; Dragoin, 1971; Wright, Foshee, and McCleary, 1971; Ader, 1973). However, it is very possible for these relationships to become obscured by floor and ceiling effects.

Nature of the Thirst Stimulus

Domjan (1975) found that the extent to which animals avoid a conditioned aversive solution depends not only on the strength but also on the source of their motivation to drink. Independent groups of rats were compared drinking in response to either water deprivation or osmotic thirst induced by intraperitoneal injections of hypertonic saline. When water or a palatable saccharin solution served as the drinking fluid, comparable fluid intakes were produced

by deprivation and osmotic thirst. However, when a saccharin solution previously associated with the aversive effects of lithium served as the drinking fluid, animals injected with hypertonic saline drank substantially less than water deprived animals.

The results showed that this hyperreactivity to a conditioned aversive flavour in animals suffering from osmotic thirst was due to the reduced palatability of the saccharin flavour rather thank its previous experience with lithium. The results also indicated that the effect was not due to differential taste-aversion learning, handling, food deprivation or weight loss before the test sessions.

Specific Hungers:

Another phenomena involving taste aversion learning besides aversion to flavours produced by toxicosis is an aversion to flavours produced by deficient-diets. Diets which are

deficient in some substances necessary for normal body function (i.e. vitamins or minerals) can be considered to be slow poisons. Rozin (1967) has shown that thiamine deficient rats display a generalized avoidance of the old-familiar deficient diet. Also, rats will avoid the familiar-deficient diet if it is presented alone and they are food deprived and perfectly healthy at the time of presentation.

Many researchers have found that animals which are deficient in a substance will choose foods containing that substance over foods lacking the substance (Harris, Clay, Hargreaves, and Ward, 1933; Richter, 1943; Scott and Quint, 1945). This phenomena has been referred to as "specific hunger."

It seems reasonable to consider specific hungers as parallel to poisoning. Evidence for this is presented in a study by Rozin (1968) in which rats were given a thiamine deficient or lithium chloride poisoned familiar food. He found that all rats showed an increased preference for a familiar safe food over the thiamine deficient or LiCl poisoned foods and a completely new diet. There were no differences between the specific hunger and poisoning groups.

Also the novelty of a taste plays the same role in specific hungers as it does in taste aversion learning. Specific hunger effects are smallest and least likely to be detected when the substance tested is familiar during the deficiency stage, but some other substance present during deficiency is novel. Conversely, specific hunger effects are largest when

the substance tested is novel during deficiency, but no other novel substance is present (Maier, Zahorik, and Albin, 1971).

Weisinger, Parker, and Skorupski (1974) found that there exists an interaction between the need state produced by a toxic agent and certain test substances in determining whether an aversion will be produced. Rats were allowed to consume either sucrose or saline prior to injections of either insulin or formalin, or by exposure to X-rays. Formalin was an effective agent in conditioning aversions to sucrose but not to saline (2 - bottle preference test) and similarly, insulin was found to be effective in producing conditioned aversions to saline but not to sucrose. X-irradiation produced a strong aversion to either solution.

If an aversion to flavours can be conditioned by toxicosis then it would seem logical to expect that an increased preference for flavours can be conditioned by beneficial after-effects. Zahorik and Maier (1969) found that pairing a taste with recovery from thiamine deficiency produced a preference for that flavour over a taste associated with deficiency and a novel taste in thiamine deficient rats. The preference persisted after recovery from deficiency. Since the rats show a preference for the taste associated with recovery from thiamine deficiency in both the deficient and nondeficient states, it appears that this taste acquired conditioned reinforcing properties.

Also Revusky (1967; Revusky and Garcia, 1970) found that

food with clear positive consequences would be preferred to foods with relatively neutral consequences. In this experiment rats were fed one nutrient solution while hungry and a different one when satiated. Both solutions were equally familiar. After five days of this training, a significant preference developed in a two-bottle test for the solution drunk while deprived.

The positive preference effects have been rather small by comparison with learned aversions, and more difficult to obtain (Revusky and Garcia, 1970). Possibly the rat is better prepared to learn aversions because rapid learning there has particular survival value; that is, mistakes are very costly.

Comparison of Learned Aversions with Operant Conditioning:

Revusky and Garcia (1970) have described taste aversion learning as operant conditioning: the distinctively flavoured substance becomes correlated with the punishment of the response of ingestion by toxicosis, therefore the probability of ingesting that substance decreases. Evidence for this is based on the fact that ingestion is affected by the various common parameters of learning in much the same way as other operants. For example, there are some cases in which a discriminative stimulus is temporally separated from the response by 24 hours and is still effective. Capaldi (1967) found that if rats are rewarded on alternate trials in a runway, they will learn to run much more slowly on nonreinforced trials than on reinforced trials even when the intertrial interval

is as long as 24 hours. Petrinovich and Bolles (1957) and Petrinovich, Bradford, and McGaugh (1965) have shown that rats can learn to alternate in a T-maze even if the intertrial interval is several hours.

In operant conditioning as in taste aversion learning, there are some instances in which stimulus relevance is an important variable. For example, Konorski (1967) found with dogs that when a task involves a directional response (go left - go right), a directional stimulus, location of the sound source, is a more effective cue than the pitch of the sound. When the task involves a discrimination between the stimuli correlated with reward and nonreward (go - no go), pitch is a more effective cue than location.

In defining ingestion as an operant Revusky and Garcia (1970) state that from known principles of operant conditioning the probability of ingestion is controlled by the amount or quality of reinforcement. As indicated earlier in the paper, the intensity of learned aversions increases as the strength of the poison increases.

Comparison of Learned Aversions With Classical Conditioning:

More frequently, learned aversions have been compared procedurally to classical conditioning (Garcia and Ervin, 1968; Zahorik and Maier, 1969): a taste CS is followed by an aversive UCS that produces an unpleasant internal state UCR. After one or more pairings the presentation of the CS alone elicits some fraction of the UCR, which is called the

conditioned response, CR. If taste aversion learning is a form of classical conditioning then the flavour which has been paired with illness should actually elicit some of the symptoms of that illness, and changes in ingestion should only be one of those symptoms.

Thiamine-deficient diet is an ideal US for such an experiment, because the symptoms of thiamine deficiency are well documented and many of these symptoms are easily measured in an intact, unanesthetized rat. Zahorik (1972) paired thiamine deficiency and temporary recovery from deficiency with distinctively flavoured drinking solutions in a procedure shown to produce aversions to the taste paired with deficiency and preferences for the taste paired with recovery (Garcia, Ervin, Yorke, and Koelling, 1967; Zahorik and Maier, 1969). Several symptoms of thiamine deficiency were measured throughout the experiment, and the data suggest that tastes paired with deficiency elicit the symptoms (heart rate, solution intake) of deficiency, while tastes paired with recovery elicit the responses seen in recovery. It should be pointed out however, that when corrections were made for the effects of familiarity of tastes on the symptoms, the results did not offer unequivocal evidence for the presence of conditioned responses to both the tastes paired with recovery and the tastes paired with deficiency.

There is another study which suggests that conditioned taste aversions are similar to classical conditioning. Dragoin (1971) conducted a taste aversion experiment using two

strains of rats, the Sprague-Dawley albino and the Long Evans hooded. The rats were conditioned to avoid distinctively flavoured fluid (HCl) by twice conditionally pairing the fluid with a drug-induced illness (injection of cyclophosphamide). The UCS followed the CS by 30 minutes. The CS and UCS were varied factorially at three levels of intensity. It was found that conditioned taste aversion is a direct function of the intensity of both the CS and the UCS. As mentioned earlier in the paper, other researchers have reported that the magnitude of an aversion to a flavour increases with the severity of the UCS (Garcia, Ervin, and Koelling, 1967; Revusky, 1968; Wright, Foshee, and McCleary, 1971). However, it is very possible for these relationships to become obscured by floor and ceiling effects.

In classical conditioning the intensity of both the CS and UCS are important variables (Kimble, 1961; Razran, 1957). The difference in performance produced by the variation in CS intensity in Dragoin's (1971) study is consistent with the findings in traditional studies of classical conditioning (Beecroft, 1966). Thus this finding supports the contention that taste aversions are indeed a form of associative learning similar, in many respects, to classical conditioning.

It should be mentioned that studies conditioning the GSR's of human subjects to tones of four different intensities found no significant effect of CS intensity upon learning (Grant and Schneider, 1949; Hovland, 1937 a, 1937 b, 1937 c). One possible complication, however, is that these studies

used humans and the studies by Beecroft (1966) Kimble (1951) and Razran (1957) used animal subjects. It is possible that the conditioned responses of human subjects may be mediated by subvocal verbal processes which, in a sense, equate the CS intensities for all groups. That is, human subjects may respond implicitly with a reaction such as, "there it is", or "the tone",which would tend to make the situation similar for all subjects regardless of the intensity of the CS.

Best (1975) found that conditioned inhibition can be established in a taste-aversion procedure. Further research is required to investigate the extent to which taste aversion learning can be described by other principles established within the classical conditioning paradigm.

Mechanisms Which Mediate Taste Aversion:

The mechanism which mediates long-interval taste aversion is not completely clear. It has been hypothesized that the CS could be retained peripherally in the form of an aftertaste. Rozin (1969) found that an aversion could be established to one of two concentrations of the same solution. Nachman (1970) found that an aversion could be established to solutions of different temperatures. Also, studies have shown that if the aftertaste of a novel solution is masked with a familiar solution before the administration of the poison, an aversion

develops to the novel solution (Farley, McLaurin, Scarborough, and Rawlings, 1964; McLaurin, Farley, and Scarborough, 1963; Revusky and Bedarf, 1967). Ahlers and Best (1971) used two highly flavoured solutions (saccharin and anise) which in a pilot study S's were found to prefer equally. The animals had been previously familiarized with one of the solutions and an aversion to the novel stimuli developed independently of the flavour of the novel solution or of the order of presentation

prior to apomorphine injection. It is possible that aftertaste may play a secondary role but these studies indicate that it does not play a necessary role in taste aversion learning.

Revusky (1971) proposed an "interference plus - belongingness" theory to explain the difference between taste aversion learning and other types of learning. Revusky explains that ordinarily a UCS is easily associable with visual, auditory, proprioceptive, and other cues. The animal is constantly hit with many of these cues, thus any increase in the delay between the would be CS and the UCS would increase the probability that another potential CS will occur before the UCS. The UCS would then be associated with these more recent interfering stimuli and not the experimental CS. In taste aversion learning, the animal ordinarily experiences very few tastes over a long delay. Consequently there is little concurrent interference to prevent association of the poison with a taste which has been presented several hours previously.

This theory although valid in part seems to predict that learning should occur with unlimited delays if there is no taste interference. Kalat and Rozin (1971) have shown that with increasing delays there is a decrease in learning even if there are no tastes available during the delay. Also, the introduction of three novel or previously poisoned interfering solutions during the delay interval does not prevent a learned aversion to a novel solution.

There are two other theories to explain what is going

on during the long delay. One is the traditional "trace-decay" view which holds that the central CS trace of a taste decays very slowly over time. The other is the "learned safety" view proposed by Kalat and Rozin (1971), which holds that during the CS-UCS delay, the rat gradually learns that the taste is safe.

Rozin and Ree (1972) found that if rats are anesthetized during the interval they can learn taste aversions with taste-poison intervals even longer than those which are usually effective. This could be explained either as a reduction in interference or as a result of safety learning.

A line of evidence favourable to the learned-safety theory, as mentioned earlier, is that if a rat drinks a novel and later a familiar taste prior to poisoning, it acquires a much stronger aversion to the novel rather than to the familiar solution (Kalat, 1971; Revusky and Bedarf, 1967; Wittlin and Brookshire, 1968). Kalat and Rozin (1973) found that if a rat drinks a novel solution for one day and then at least three weeks later is given this solution again followed by poisoning he accepts the solution as familiar and safe. They also found that during the CS-UCS interval if a rat drinks a solution twice before a single poisoning, it learns less aversion than if it received only the second presentation. (Bolles, Riley, and Laskowski, 1973).

The results of experiments by Domjan and Bowman (1974) show that the experimental design proposed by Kalat and Rozin (1973) does not provide adequate evidence to suggest a large

contribution of learned safety to the CS-UCS delay gradient. Domjan and Bowman found that a second presentation of the CS during conditioning may (1) enhance subsequent intakes of the CS solution whether or not subjects are poisoned, and/or (2) facilitate aversion learning, the facilitory effect being greater if the second CS exposure occurs closer to poisoning. They point out that it is not clear how the learned safety hypothesis could be modified to explain the facilitory effects on aversion learning of a second presentation of the CS during conditioning. The trace decay and concurrent interference hypotheses (Revusky, 1971) can explain this effect and are consistent with much of the evidence on taste-aversion learning. With the trace-decay mechanism, the second presentation of the CS during an extended CS-UCS interval would cause stronger taste aversion learning because it strengthens the memory of the CS just prior to poisoning. The concurrent interference hypothesis suggests that the second exposure to the CS would reduce the number of possible interfering stimuli experienced between the last presentation of the CS and poisoning and thus would produce greater aversion learning.

The findings of Bond and DiGiusto (1975) suggest that the Kalat and Rozin (1973) "learned-safety" theory may need to be extended. Their investigation showed that when a rat receives two presentations of the same solution before poisoning the "learned-safety" theory is supported if the rat consumes more of the solution on the first presentation or equal amounts on both presentations. However, if the rat consumes more of the

solution on the second presentation, the "learned-safety" effect is eliminated. Bond and DiGiusto explain that this suggests that the rats were able to "reassess safety" as a result of the increased amount of solution presented on the second occasion. This finding also provides further evidence to indicate that the strength of an aversion to a solution is a direct function of the amount of solution consumed prior to poisoning (Bond and DiGiusto, 1975; Bond and Harland, 1975).

Strain Differences in Taste Aversion Learning:

In Dragoin's (1971) study, mentioned earlier, the Sprague-Dawley albino and the Long Evans hooded strains of rats were used. The Long Evans hooded rats have been reported as having a significantly higher level of exploratory behaviour, avoidance learning, and arousal than the Sprague-Dawley albino rats (Carr and Williams, 1957; Schaefer, 1959; and Foshee, 1960). The Long-Evans hooded rats in Dragoin's experiment drank less of the distinctively flavoured solution on all test presentations than the Sprague-Dawley albino rats, however, the difference on the first test trial was not significant. After two CS - UCS pairings the difference was significant. The strain difference persisted on the last four extinction trials, and on the final day of extinction, the Sprague-Dawley rats completely extinguished while the Long-Evans rats were still significantly lower. Dragoin mentions several hypothesis regarding the source of the strain differences. Perhaps the rats are differentially sensitive to the gustatory cue or have

different internal reactions to the cyclophasphamide. As has been shown the CS and UCS intensity is an important variable. Perhaps the hypothesized central mechanism underlying this learning (Garcia and Ervin, 1968) has been differentially modified by the various breeding programs producing these strains. On the basis of this data, Dragoin states that no firm conclusion can be made concerning the source of the strain difference. It should be pointed out, however, that the two strains of rats were procured from different commercial sources. Thus the question of strain differences is equivocal.

Ader (1973) found no differences in taste aversion learning between the Sprague-Dawley and Long Evans animals that were obtained from the same commercial supplier. However, the Sprague-Dawley rats that were obtained from ARS/Sprague-Dawley showed a greater initial aversion and a more sustained response than the other two strains. Differences between original breeding stock, breeding programs, as well as conditions of husbandry that prevail among commercial suppliers of laboratory animals could contribute to differences in behaviour. Thus whether or not there are differences in illness-induced taste aversion as a function of genotypic differences between domesticated strains of rats remains unanswered.

Purpose of Present Investigation:

Learning is a phenotype and there has been much research using learning to seek the genetic bases for behavioral differences. There have been observed large genetic differences

in learning and this has led to the search for the source of these differences as well as their generality to other categories of learning. In order to carry out this kind of genetic analysis, the characteristics of either pure bred strains or selectively bred animals must be investigated.

A summary of strain differences in learning rate, responses to selective breeding for learning, heritabilities of learning phenotypes, and heterosis and overdominance are given in Wahlsten's (1972) article. He also has reviewed the methods that have been employed to study the genetic correlates of learning and various processes (sensory capacities and preferences, motivation, memory, emotionality, nervous system) which are involved in learning. As well, Wahlsten has provided a summary of the findings related to the

generality of learning differences.

Wahlsten has pointed out that "it is worthwhile to determine precisely what mechanisms or components of the learning process are modified in different genotypes and thereby yield the observed phenotypic differences (p. 152)." He also emphasizes that researchers should try to determine that "if there exists a finite set of mechanisms that result in overt learning, are all of these mechanisms affected by genetic variation, or are certain components of the learning process more likely to be changed than others?" (p. 152).

In this context the main purpose of this study is to investigate genotype-dependent development of taste aversion. It attempts to seek information on some of the factors involved in taste aversion learning in bidirectionally, selectively bred strains of rats. The use of bidirectionally, selectively bred strains of rats can assure the control of the genetic bases and the stability of contrasting behavioral components (Bignami, 1965; Broadhurst 1960, Tryon, 1940). Therefore there is an advantage in using these strains in the study of taste aversion learning. Little research has been done in this area.

It is proposed to use the Maudsley nonreactive (MNR) and the Maudsley reactive (MR) strains of rats that were designated by Jay (1963), and the Roman high-avoidance (RHA) and the Roman low-avoidance (RLA) strains designated by Broadhurst and Bignami (1965). The MNR and MR strains were

developed by means of selective breeding for extreme defecation score in open-field test of emotional reactivity by Broadhurst (1960). The breeding of the RHA and RLA conditioning strains was initiated by Bignami (1965) for high and low rates of two-way active-avoidance conditioning. These selectively bred strains have been redesignated by Satinder (1971) as MNR/Har/Lu, MR/Har/Lu, RHA/Lu, and RLA/Lu, to differentiate the strains at Lakehead University from the strains at the other places. This was done similar to the standardized nomenclature used on mice strains (Staats, 1968). It is proposed to use a control strain randomly bred from the same stock of animals as the parental generation of the RHA/Lu and RLA/Lu strains and this is designated as RCA/Lu.

The RHA strain (Bignami, 1965; Broadhurst and Bignami, 1965; Satinder, 1971, 1972) and the MNR strain (Broadhurst and Levine, 1963; Joffe, 1964; Levine and Broadhurst, 1963; Owen, 1963; Savage and Eysenck, 1964) are both superior in escape - avoidance conditioning and they do not resemble each other in respect of a low open-field defecation score (Broadhurst and Bignami, 1965; Broadhurst, 1970). Similarly, the RLA and MR strains, while low in escape - avoidance conditioning, do not resemble each other in respect of a high open-field defecation score.

Some researchers have found that the RHA strain is significantly more active in exploratory ambulation than the RLA strain, just as the MNR is more active than the MR strain (Broadhurst, 1966; Broadhurst and Bignami, 1965). Also

Satinder (1971, 1972) has pointed out that the RHA/Lu strain is significantly more active in terms of intertrial crossings (ITC) in two-way avoidance conditioning than the RLA/Lu strain. Thus it is possible that genetic selection was for increased general activity in the RHA/Lu strain which may have indirectly produced superior performance in a two-way active avoidance conditioning task. Satinder and Hill (1974) tested these strains for general activity in a neutral situation independent of a conditioning task. They found that the RLA/Lu strain is slightly more active than the RHA/Lu strain but the differences are not significant. Thus the differences between the RHA and RLA strains in two-way active avoidance cannot be accounted for in terms of increased general activity of the RHA strain.

Perhaps, the strain differences in avoidance conditioning could be due to motivational differences between the strains. Satinder and Hill (1974) and Satinder and Petryshyn (1974) found that the RHA/Lu and RLA/Lu strains, in fact, differed in foot-shock sensitivity.

Satinder and Petryshyn (1974) tested these strains using equivalent states of aversive motivation as UCS levels. Aversive motivation was calculated by measuring the flinch, jump and fleeing responses to electric foot-shock between the strains. They found that the use of equivalent aversive motivational states as UCS levels accounted for only part of the variation in learning rates between these strains. This

indicated that the motivational differences between these strains of rats are not the only determinants of avoidance behaviour. This finding is in general agreement with Wahlsten's (1972) study using sensitivity and response topography to electric shock in inbred and F_1 hybrid mice strains for jump-out and one-way avoidance tasks.

Satinder and Petryshyn (1974) observed that the RHA/Lu strain responds by flight from the aversive situation and the RLA/Lu strain freezes on the safe bars of the electric grid in responses to the same aversive stimulus. Satinder and Petryshyn (1974) found "that where the response topography (fleeing) was most compatible for escape and effective avoidance there were no differences at all between the strains in the number of animals learning to avoid." However, "where the level of response topography to electric shock was not assured for effective escape and consequent avoidance, the RLA/Lu strain learned consistently at a lower rate than the RHA/Lu strain." It appears that for the RLA/Lu strain when the strength of the fear and fleeing response becomes greater than the freezing response the probability of an avoidance response increases. Satinder and Petryshyn (1974) found that the RLA/Lu strain under different levels of UCS showed noticeable differences in learning rates compared with the RHA/Lu strain which under different levels of UCS did not show any appreciable differences.

The difference between the RHA/Lu strain and the RLA/Lu strains selectively bred for high and low rates of two-way

active avoidance learning are generizable to one-way active avoidance learning. Satinder and Petryshyn (1974) found that the RHA/Lu strain had a significantly higher one-way active avoidance score than the RLA/Lu strain.

Satinder and Petryshyn (1974) in comparing two-way (Satinder, 1971, 1972) and one-way active avoidance, gained some insight into the possible mechanisms for the observed differences in avoidance behaviour of the RHA/Lu and RLA/Lu strains. Satinder (1971 and 1972) found that in two-way active avoidance, the RHA/Lu strain shows a very high degree of learning over 5 days of training and the RLA/Lu strain shows a very low degree of learning. Under the effects of d-amphetamine (Satinder, 1971, 1972) and caffeine (Satinder, 1971) the RHA/Lu animals show a general suppression or no change and the RLA/Lu animals show a general facilitation in avoidance behaviour, thus bringing the two strains closer.

Experiments with one-way active avoidance indicate that both the RHA/Lu and RLA/Lu strains show significant learning over 3 days of training although the RHA/Lu strain is consistently higher than the RLA/Lu strain (Satinder and Petryshyn, 1974). Under the effects of d-amphetamine the strain differences practically disappear.

Satinder and Petryshyn (1974) point out that "this information from the two-way and one-way active avoidance behaviour and its modification by d-amphetamine provide reasonably convincing evidence to propose that RHA/Lu and

RLA/Lu strains differ on an inverted - U shape arousal function." The authors explain that this is due to the fact that the one-way task is less complex in nature than the two-way task (Anisman, 1973; Anisman and Waller, 1972; Ashe and McCain, 1972; Theios and Dunaway, 1964) and on these two tasks the avoidance performance of these strains indicate that RHA/Lu has a relatively high level of arousal compared with the RLA/Lu strain. It seems reasonable to believe that an organism with a low level of arousal will have a poor performance on a complex task compared with an organism with a relatively higher level of arousal, and for a simple task the organism with a low level of arousal has a better performance than on a complex task. Also if the organisms with the low and high levels of arousal are induced to higher levels of arousal then the organism with the initial low level of arousal will improve in performance on a complex and simple tasks, and the organism with the initial high level of arousal will either deteriorate or show a plateau in performance on both complex and simple tasks. Satinder and Petryshyn (1974) point out that this does represent the performance of the RLA/Lu and RHA/Lu strains respectively, under the effects of d-amphetamine in both two-way and one-way avoidance tasks.

It appears that genetic differences in avoidance learning rates of the RHA/Lu and the RLA/Lu strains are not due to differences in general activity between the strains. The motivational differences due to differential shock sensitivity do not explain entirely the differences in avoidance learning

between the strains. Also, it is possible that the differences in avoidance learning are partly due to differences in the level of arousal in the RHA/Lu and RLA/Lu strains.

Several investigations have shown that the MR strain defecate significantly more than the MNR strain in the open-field test of emotionality (Blizard, 1970; Broadhurst and Bignami, 1965; Broadhurst and Eysenck, 1965; Gray, Levine, and Broadhurst, 1965; Harrington, 1972; Imada, 1970; Joffe, 1965; 1969; Powell and North-Jones, 1974; Rick and Fulker, 1972). Blizard (1970) found that the defecation scores of these strains in the open-field test seem unrelated to their normal levels in the home cage and also to their digestive transit times.

Extensive research concerning the behavioral and physiological characteristics of these strains have suggested that the MR strain is more susceptible to the arousal of fear and more emotionally responsive than the MNR strain (Blizard 1971; Broadhurst, 1975; Eysenck, 1964; Eysenck and Broadhurst, 1964; Ferraro and York, 1968; Imada, 1972; Singh, 1959; Singh and Eysenck, 1960).

In determining the genetic differences in avoidance learning rates of the MNR and MR strains some researchers (Broadhurst and Levine, 1963; Levine and Broadhurst, 1963; Owen, 1963; Joffe, 1964; Savage and Eysenck, 1964) have hypothesized that the emotionality of the MR strain would tend to lead to inactivity which impedes the motor responses required and hence the MR strain would be at a disadvantage

in escape avoidance conditioning. Levine and Broadhurst (1963), Broadhurst and Bignami (1965), and Wilcock and Broadhurst (1967) have shown that the activity level and the number of avoidance responses of rats are positively correlated. In experiments by Singh (1959) and Singh and Eysenck (1960), conditioned suppression, which is presumably less effected by activity level than avoidance conditioning, was used as a primary index of emotionality. The results showed that the MR strain was superior in the formation of conditioned emotional responses. This study, however, primarily tests emotionality and consequently does not indicate that the MR strain is superior in a conditioning task in which activity level is presumably not a factor. More research is needed to determine if the strain differences in avoidance learning could be due to the increased general activity of the MNR strain.

Broadhurst and Levine (1963) argued that in avoidance conditioning the MR strain, through heightened emotionality, acquired an interfering response to shock, such as "freezing". Wilcock (1968) found that no such inactivity is characteristic of the MR strain's motor response to shock.

Perhaps the genetic differences in avoidance learning rates of the MNR and MR strains are due to differences in conditionability (intelligence) between the strains. Several investigations have shown that the MR strain performed better in Hebb-Williams maze learning than the MNR strain indicating that the MR strain has greater intelligence or conditionability (Garg and Holland 1967, 1968, and 1969; Garg 1970).

Another study found no significant differences among these strains in Hebb-Williams maze performance (Das and Broadhurst, 1959).

Imada (1972) demonstrated that the MNR, MR, and RHA strains did not differ in conditionability and that the RLA strain had poorer conditionability than the other three strains. This study measured the degree of suppression of water-drinking behavior by unsignaled electric shock (emotionality), and the rate of recovery of drinking behavior when the unsignaled shock became signaled shock (conditionability). In the conditioning stage of this experiment the shock intensity administered was set so that the average degree of suppression of water drinking was equal in all four strains. The study showed that the RLA strain's rate of recovery of drinking behavior was significantly lower than that of the other three strains which did not differ among one another. This study also provided further evidence to indicate that the MR rats were the most emotional, the MNR rats were the least emotional, and the two Roman strains were intermediate.

In an investigation using light reinforcement the MNR strain in a Skinner Box appeared to have higher conditionability than the MR strain (Weldon, 1968). The MNR pressed the light-bright and light-onset levers more frequently than the MR strain; whereas the MR strain pressed the light-offset and dummy levers more often than the MNR strains. Some possible explanations are that the MNR strain was more reinforced by the stimulus change than the MR strain or that the MR strain found the light

more aversive than did the MNR strain". In general, due to the varied results in conditioning studies it appears that genetic differences in avoidance learning rates of the MNR and MR strains cannot be accounted for in terms of conditionability or "intelligence".

Perhaps the strain differences in avoidance conditioning could be due to motivational differences between the strains. Wilcock (1968) and Satinder (1976) found that the MNR/Har/Lu and MR/Har/Lu strains did not differ in foot-shock sensitivity. Consequently, it appears that the genetic differences in avoidance learning are not due to motivational differences caused by differential shock sensitivity.

Thus it appears that the genetic differences in avoidance learning rates of the MNR and MR strains are not due to differences in conditionability or "intelligence" between the strains. More research is needed to determine if the differences in avoidance conditioning could be due to the increased general activity of the MNR strain. The genetic differences in avoidance learning are not due to motivational differences caused by differential shock sensitivity. There has been no research to determine if differences in the level of arousal in the MNR and MR strains could explain the differences in avoidance learning.

Summary:

It is at present not known whether in fact classical and instrumental learning are two distinct processes or different

reflections of the same basic learning process (Miller, 1969; Rescorla and Solomen, (1967). For example, the belief that instrumental learning is possible only for the cerebrospinal system and, conversely, that the autonomic nervous system can be modified only by classical conditioning has been used as one of the strongest arguments for the notion that instrumental learning and classical conditioning are two basically different phenomena rather than different manifestations of the same phenomena under different conditions. However, studies have shown that instrumental learning of visceral responses (such as, salivation, heart rate, intestinal contractions, etc.) is possible (Banuazizi, 1972; Headrick, Feather, and Wells, 1971; Miller and Carmona, 1967; Scott, Peters, Gillespie, Blandchard, Edmunson, and Young, 1973).

There are a number of ways in which operant and classical conditioning can be seen as two distinct processes. In instrumental learning the experimenter's presentation of the reinforcer is dependent upon the organism's behavior, but in classical conditioning it is independent of that behavior. In classical conditioning the reinforcement is made contingent upon the occurrence of a stimulus; in instrumental training it is made contingent upon the occurrence of an arbitrarily selected response. For many common responses there is no practical difficulty in identifying which are operants and which are respondents, however there are cases where this is extremely difficult. Also it appears that the reinforcers for classical conditioning are closely related to reinforcers

for instrumental conditioning.

As indicated earlier in the paper the mechanism which mediates long-interval taste aversion is not completely clear. However, taste aversion is a form of associative learning, similar in many respects to classical conditioning. Since it is not known whether classical and instrumental learning are two distinct phenomena or different manifestations of the same phenomena under different conditions, it seems reasonable to expect that an organism that is superior in an operant type of conditioning may also be superior in a classical type of conditioning. It was hypothesized in the present investigation that the RHA/Lu and the MNR/Har/Lu strains of rats which are superior in avoidance conditioning would perhaps be superior in taste aversion conditioning compared to the RLA/Lu and MR/Har/Lu strains. Also the RHA/Lu strain which has the highest learning ability in avoidance conditioning might also have the highest learning ability in taste aversion conditioning, while the RLA/Lu strain which has the lowest learning ability in avoidance conditioning would be the lowest in taste aversion learning. The relationship between avoidance conditioning and taste aversion learning seem uncertain in view of the fact that in a passive type of learning, similar

in this respect to taste aversion learning, the MNR, MR, and RHA did not show differences in conditionability (Imada, 1972). However, the RLA did show a lower conditionability than these strains.

In the light of the observations by Wahlsten (1972), mentioned earlier in the paper, this study investigates (i) the question of generality of the genetically selected behavior of avoidance conditioning to taste aversion conditioning; and (ii) the mechanisms or components of taste aversion learning which are modified in different genotypes by measuring the taste preferences, amount of CS consumed prior to poisoning, and sensitivity to the UCS among the strains.

In this study the classical conditioning model of learned taste aversions is also investigated. If the classical conditioning model is accepted, it would predict that the flavour which has been paired with illness should actually elicit some of the symptoms of the illness. As mentioned earlier, Zohorik (1972) did not find unequivocal evidence for the presence of conditioned responses to both tastes paired with thiamine deficiency and tastes paired with recovery (Zahorik, 1972).

If the hypothesized strain differences exist in taste aversion conditioning and if these differences are not due to differences in taste preference or the amount of CS consumed prior to poisoning, then this study will provide evidence to suggest that the RLA/Lu and MR/Har/Lu strains have poorer conditionability than the RHA/Lu and the MNR/Har/Lu strains of rats.

EXPERIMENT 1

Method:

Experimental Design:

Experiment 1 consisted of three groups of rats (Groups A, B, and C). This experiment assessed the amount of conditioned taste aversion among five strains of rats to a novel solution when followed by an injection of 6 ml./kg. of a solution of .4 molar lithium chloride (Groups A and B) and .7 molar lithium chloride (Group C). Kalat and Rozin (1973) provide evidence to indicate that a dosage of 6 ml./kg. of .15 M LiCl is effective in conditioning taste aversion. A control study is carried out in Experiment 2.

An assessment was made of the differences among the five strains in sensitivity to the UCS by measuring the symptoms that occurred among these strains during toxicosis. This experiment also investigated the classical conditioning model of learned taste aversion by determining whether a novel flavour which has been paired with toxicosis will elicit some of the symptoms of the illness.

There were four acquisition trials (CS-UCS pairings) for all groups and five extinction trials for Group A and nine extinction trials for Groups B and C. The novel solution was a 5% sugar solution and the familiar solution was distilled water. The animals were given access to Purina Rat Chow ad lib and were deprived of water for 23 hours and 40 minutes each day.

Prior to this experiment a pilot study was conducted. The purpose of this study was to construct a scale of the symptoms of the illness induced by the injection of lithium chloride. A dose of 6 ml. of .12 M lithium chloride produces occasional diarrhea and mild ataxia in a rat lasting 45-60 minutes. (Domjan and Wilson, 1972).

The pilot study showed that the symptoms for .4 M Li Cl and .7 M Li Cl included: (1) the rat lying down with his head down, (2) the rat's eyes less than a half open, and (3) diarrhea. (See Symptom Recording Sheet Appendix - P.89) The illness period for both doses of Li Cl lasted approximately 70 to 85 minutes.

Subjects:

The subjects were sixty naive rats, equally represented by each sex, and 12 each from MNR/Har/Lu, MR/Har/Lu, RHA/Lu, RLA/Lu, and RCA/Lu strains. The experimental design was a 5 x 2 factorial design. There were 6 males and 6 females from each strain in the treatment group. Each of the groups A, B and C consisted of 20 rats, 4 from each of the strains, and equally represented by each sex. The animals were all bred and reared in the laboratory, weaned at 28 days, and were 100 days of age at the start of the experiment. Before experimentation the animals were housed in groups of two or three of the same sex and the strains were maintained on separate cage racks. During the course of experimentation the animals were code numbered and housed in individual cages

on the same rack. Before experimentation the animals were given ad lib access to tap water and Purina Rat Chow. The laboratory temperature was thermostatically controlled within the range of 22 $\pm$ 1°C and the humidity level was maintained at 40%. Fluorescent lights were on from 9:00 a.m. to 9:00 p.m.

Apparatus:

The experiment was carried out in the home cage. The home cage was a stainless steel 10 x 7 x 7 in. It was fixed with one metal holder and one calibrated fluid bottle in the front and outside of the cage. A food hopper was fixed on the inner back wall of the cage. The food hopper perfectly protected the food from any contamination from urine or feces. The novel stimulus was a 5% sugar solution and the familiar stimulus was distilled water. The fluids were always presented at room temperature.

Procedure:

The experimental paradigm consists of three phases for each of the three groups. In the first phase (the familiar solution phase) the animals were first weighed and then allowed a 20 min. access to a bottle of distilled water (the familiar solution) at the same time each day for six days. At the end of the drinking period the amount of fluid consumed was recorded.

The conditioning phase took place on Days 7, 10, 13 and 16. The test phase took place on Days 10, 13, 16 and 19. On

each of these days the rats were weighed and then allowed a 20 min. access to a bottle of the novel solution at the same time of day as each of the familiar solution trials. The amount of fluid consumed was recorded. Except on Day 19 forty-five minutes after the end of the drinking period each rat received an injection of 6 ml./kg. of .4 M lithium chloride (Groups A and B) and .7 M lithium chloride (Group C). Following each of the conditioning trials and/or testing trials the rats were allowed two recovery days. On each of these days, the rats were weighed and then given a 20 minute access to a bottle of the familiar solution at the same time of day as each of the conditioning and/or testing trials.

Five extinction trials (for Group A) and nine extinction trials (for Groups B and C) were then given to the rats within the same paradigm. The extinction trials took place on Days 22, 25, 28, 31, and 34 for Groups A, B, and C and also on Days 37, 40, 43, and 46 for Groups B and C. On each of these days the rats were weighed and then allowed a 20 minute access to a bottle of novel solution at the same time of day as each of the conditioning trials. The amount of fluid consumed was recorded. (No injections were given). Following Day 19 and the first four extinction trials for Group A, B, and C and the first eight extinction trials for Groups B and C, the rats were given two familiar solution days. On each of these days, as on the recovery days, the rats were weighed and then allowed a 20 minute access to a bottle of the familiar solution at the same time of day as each of the conditioning

trials.

The symptoms of "the rats' eyes less than half open" and "the rats' lying down with their heads down" were recorded during the following times: (a) on the first and second conditioning trials (days 7 and 10) for Groups A, B, and C once every 2 minutes for 20 minutes commencing 45 minutes after the injection of lithium chloride; (b) on recovery days 9 and 11 for Group A every 2 minutes for 20 minutes commencing 45 min. after the time that the injections would have been given had these been conditioning trials. The presence or absence of the symptom of "diarrhea" was noted at the end of the above 20 min. periods.

The three symptoms were also recorded for Group A during the drinking periods on the first four conditioning trials, on the fourth test trial, on each of the recovery days in between the first four conditioning trials, and on the last day of the familiar solution phase (Day 6). The symptoms of "the rats' eyes less than half open" and"the rats' lying down with their heads down" were recorded once every four minutes during each of the above drinking periods commencing one minute after the beginning of the drinking period. The presence or absence of "diarrhea" was recorded at the end of each of these drinking periods.

Results and Discussion:

The following measures were obtained from each animal: (a) the amount of familiar solution consumed each day during

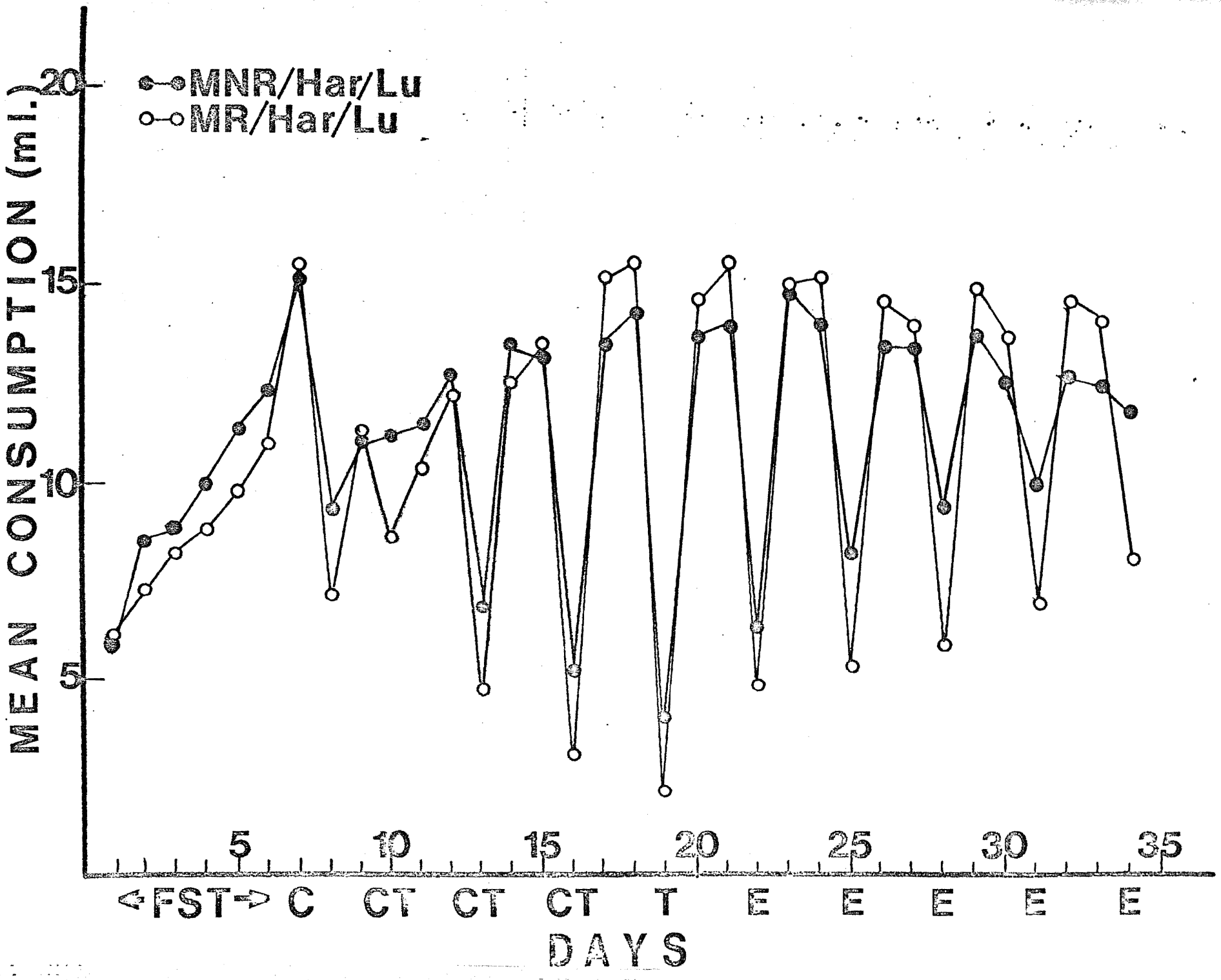
the familiar solution phase and on the recovery days; (b) the amount of novel solution consumed each day during the conditioning and testing phases; (c) the amount of familiar or novel solution consumed on each day of the extinction period; and (d) the number of symptoms from the scale of symptoms established in the pilot study that were recorded during the times mentioned above. All the results were evaluated by an analysis of variance. The only differences that were considered significant were those with associated probabilities less than .01.

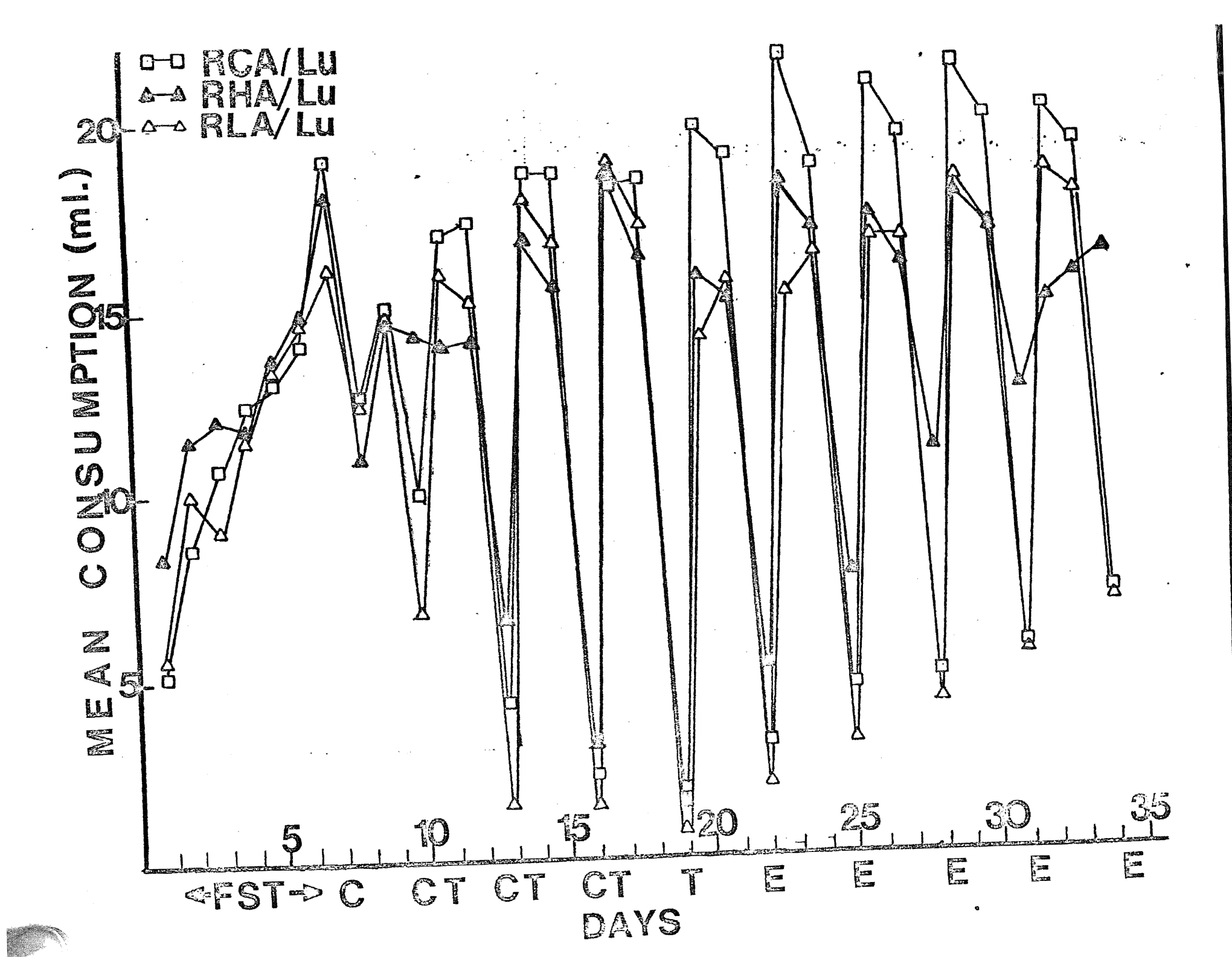
Satinder (1972) found that there are significant body weight differences between the MNR/Har/Lu, MR/Har/Lu, RCA/Lu, RHA/Lu, and RLA/Lu strains. The results were therefore analysed for both corrected body weight and absolute body weight. The results are presented only for absolute body weight because body weight differences are the integral part of strain differences.

When Groups A and B were compared to Group C no significant effects for the increased dosage of LiCl were found. For this reason the results of Groups A, B and C were pooled and evaluated together.

The mean volume of the liquids consumed during each day of the experiment for all the groups of rats are presented in Figure 1. The magnitude of conditioned taste aversion was calculated by comparing the amount of novel solution consumed during each of the testing trials with the amount of novel solution consumed on conditioning trial 1 (Day 7) for each

Figure 1 and Figure 1a: The mean volume of the liquids consumed for the five strains of rats during each day of Experiment 1 for all the groups. The Familiar Solution Trials (FST) occurred on days 1 to 6 (the familiar solution phase). There was one conditioning trial (C) on day 7, three conditioning and test trials (CT) on days 10, 13 and 16, and one test trial (T) on day 19. Five extinction trials (E) took place on days 22, 25, 28, 31 and 34.


MNR/Har/Lu
MR/Har/Lu
MEAN CONSUMPTION (ml.)
20
15
10
5
5
10
15
20
25
30
35
FST
C
CT
CT
CT
T
E
E
E
E
E
DAYS


RCA/Lu
RHA/Lu
RLA/Lu
MEAN CONSUMPTION (ml.)
20
15
10
5
5
10
15
20
25
30
35
<FST> C CT CT CT T E E E E E
DAYS

animal. Each of the strains of rats drank significantly less of the novel solution on each of the test trials than they did on conditioning trial 1 indicating that the strains displayed taste aversion learning on each test trial. (see Table 1).

Figure 2 summerizes the intake of novel solution for each strain over the four test trials. The results indicate that there are strain differences in taste aversion learning. The RLA/Lu and the MR/Har/Lu strains were superior in taste aversion learning compared to the RHA/Lu and MNR/Har/Lu strains. The RLA/Lu strain displayed the greatest magnitude of taste aversion learning compared to the other four strains and the MNR/Har/Lu strain showed the lowest degree of taste aversion learning. The RCA/Lu strain was intermediate between the RHA/Lu and RLA/Lu strains in the magnitude of taste aversion learning.

In general, the mean consumption of novel solution for each strain decreased with each subsequent test trial. Thus each of the strains learned more with each successive pairing of the CS and UCS.

The degree of taste aversion learning of the RHA/Lu and RLA/Lu strains came closer together on each subsequent test trial. The RCA/Lu strain also came closer to the RHA/Lu and RLA/Lu strains in mean consumption (except on the fourth test trial.) The fact that the mean consumption of these strains came closer together with each subsequent test trial suggests that after a number of trials all of these strains would show the same magnitude of taste aversion learning. It should be pointed out, however, that these results may possibly be

T A B L E 1

ANALYSIS OF VARIANCE FOR ALL GROUPS OF RATS

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F ratio
Over all conditioning and/or test trials						
Sex	1,10	0.0	1.7	0.2	0.6	2.2
Trial	4,40	95.9*	99.9*	102.4*	150.4*	96.3*
Interaction	4,40	1.4	7.2*	10.5*	4.4*	6.2*
Between conditioning trial 1 and test trial 1						
Sex	1,10	2.3	24.4*	8.7	9.3	0.1
Trial	1,10	43.7*	35.0*	30.5*	20.4*	51.3*
Interaction	1,10	0.3	0.0	4.2	0.2	12.4*
Between conditioning trial 1 and test trial 2						
Sex	1,10	0.0	11.0*	2.4	5.0	1.5
Trial	1,10	174.1*	88.3*	208.7*	89.7*	131.0*
Interaction	1,10	2.1	3.1	29.4*	0.7	6.3
Between conditioning trial 1 and test trial 3						
Sex	1,10	0.0	10.3*	6.9	0.8	2.5
Trial	1,10	116.4*	169.6*	276.2*	215.8*	150.0*
Interaction	1,10	1.0	9.6	24.9*	7.0	5.3
Between conditioning trial 1 and test trial 4						
Sex	1,10	0.1	7.8	4.4	1.0	2.9
Trial	1,10	229.5*	194.8*	246.3*	507.6*	176.6*
Interaction	1,10	0.6	7.4	23.3*	11.4*	5.5

* $p < .01$

Figure 2: The mean volume of novel solution consumed for the five strains of rats over the four test trials for all groups.

MEAN CONSUMPTION (ml.)
5
10
FOUR TEST TRIALS
MNR/Har/Lu
MR/Har/Lu
RCA/Lu
RHA/Lu
RLA/Lu

obscured by floor effects. That is, the strain differences disappear due to the fact that the strains have reached the highest magnitude of taste aversion learning possible (i.e. mean consumption of novel solution is close to zero).

To investigate the possibility of an illness-induced neophobia the following comparisons were made for each animal: (a) the amount of familiar solution consumed on Days 6, 9, and 12 was compared to the amount consumed on Days 8, 11, 14 respectively (see Table 2); (b) the amount of solution consumed on the first three conditioning trials was compared to the consumption on the respective first recovery days for each of these conditioning trials (see Table 3); (c) the amount of solution consumed on the first three conditioning trials was compared to the consumption on the respective days before each of these conditioning trials (see Table 4).

The fact that the MNR/Har/Lu, MR/Har/Lu, and RHA/Lu strains consumed significantly less of the familiar solution on Day 8 than on Day 6 (see Table 2) suggests that there could be an illness induced neophobia for these strains on Day 8. However, it is possible that the decreased consumption on Day 8 is compensatory, that is the MNR/Har/Lu, MR/Har/Lu, and RHA/Lu strains consumed significantly more novel solution on conditioning trial 1 and hence less familiar solution on Day 8.

The amount of novel solution consumed on conditioning trial 2 (Day 10) was not significantly different from the

TABLE 2

ANALYSIS OF VARIANCE FOR ALL GROUPS OF RATS

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F rati
Between day 6 and day 8						
Sex	1,10	8.5	2.9	12.9*	38.7*	0.0
Trial	1,10	33.1*	50.0*	2.3	10.3*	5.8
Interaction	1,10	0.0	11.1*	1.1	0.0	0.4
Between day 9 and day 11						
Sex	1,10	19.2*	5.8	9.6	34.0*	3.3
Trial	1,10	1.0	1.0	5.8	0.9	2.3
Interaction	1,10	0.1	1.3	0.7	0.9	1.2
Between day 12 and day 14						
Sex	1,10	8.1	6.4	34.3*	47.6*	4.2
Trial	1,10	1.1	1.4	2.4	19.3*	13.7*
Interaction	1,10	0.0	6.8	0.0	1.9	0.8

* $p < .01$.

TABLE 3

ANALYSIS OF VARIANCE FOR ALL GROUPS OF RATS

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F rati
Between conditioning trial 1 and day 8						
Sex	1,10	4.1	4.8	14.4*	17.5*	1.6
Trial	1,10	245.4*	110.1*	42.7*	140.6*	11.2*
Interaction	1,10	1.3	10.3*	4.8	2.4	4.4
Between conditioning trial 2 and day 11						
Sex	1,10	8.3	7.2	2.6	9.6	0.3
Trial	1,10	0.0	1.3	25.5*	0.2	60.9*
Interaction	1,10	0.6	1.3	2.8	0.2	13.1*
Between conditioning trial 3 and day 14						
Sex	1,10	1.3	1.0	1.8	14.7*	0.0
Trial	1,10	53.5*	55.6*	192.2*	70.9*	281.6*
Interaction	1,10	5.1	0.4	25.6*	3.5	6.1

* $p < .01$.

TABLE 4

ANALYSIS OF VARIANCE FOR ALL GROUPS OF RATS

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F ratio
Between conditioning trial 1 and day 6						
Sex	1,10	9.0	28.1*	44.9*	15.2*	2.9
Trial	1,10	46.6*	69.8*	23.2*	11.0*	3.5
Interaction	1,10	1.5	0.9	1.1	0.8	5.4
Between conditioning trial 2 and day 9						
Sex	1,10	16.4*	10.7*	1.6	12.5*	1.4
Trial	1,10	0.1	12.4*	19.9*	0.3	42.7*
Interaction	1,10	0.8	0.3	2.2	2.2	7.7
Between conditioning trial 3 and day 12						
Sex	1,10	1.8	3.7	2.9	8.0	0.6
Trial	1,10	87.0*	63.0*	139.2*	37.0*	403.8*
Interaction	1,10	11.3*	2.9	22.0*	1.4	20.8*

* $p < .01$.

amount of familiar solution consumed on Day 9 for the MNR/Har/Lu and RHA/Lu strains and on Day 11 for the MNR/Har/Lu, MR/Har/Lu and RHA/Lu strains. Thus there is a possibility of an illness induced neophobia for the MNR/Har/Lu and RHA/Lu strains on conditioning trial 2, Day 9, and Day 11, and for the MR/Har/Lu strain on conditioning trial 2 and day 11. It should be pointed out that the MNR/Har/Lu and RHA/Lu strains' low intake on Day 9 could still be compensating for the large amount consumed on conditioning trial 1. The fact that the MR/Har/Lu, RCA/Lu, and RLA/Lu strains consumed significantly less novel solution on test trial 1 than familiar solution on Days 9 and 11 provides further evidence to indicate that taste aversion learning occurred for these strains on this test day.

The RHA/Lu and RLA/Lu strains consumed significantly more distilled water on Day 14 than on Day 12. This is probably compensatory, that is, they consumed significantly less on conditioning trial 3 (Day 13) hence more on Day 14. There was no evidence for neophobia from the third conditioning trial onwards since all of the strains consumed significantly less novel solution on conditioning trial 3 than distilled water on both Days 12 and 14. This also provides further evidence to indicate that all of the strains displayed taste aversion learning on the third conditioning trial.

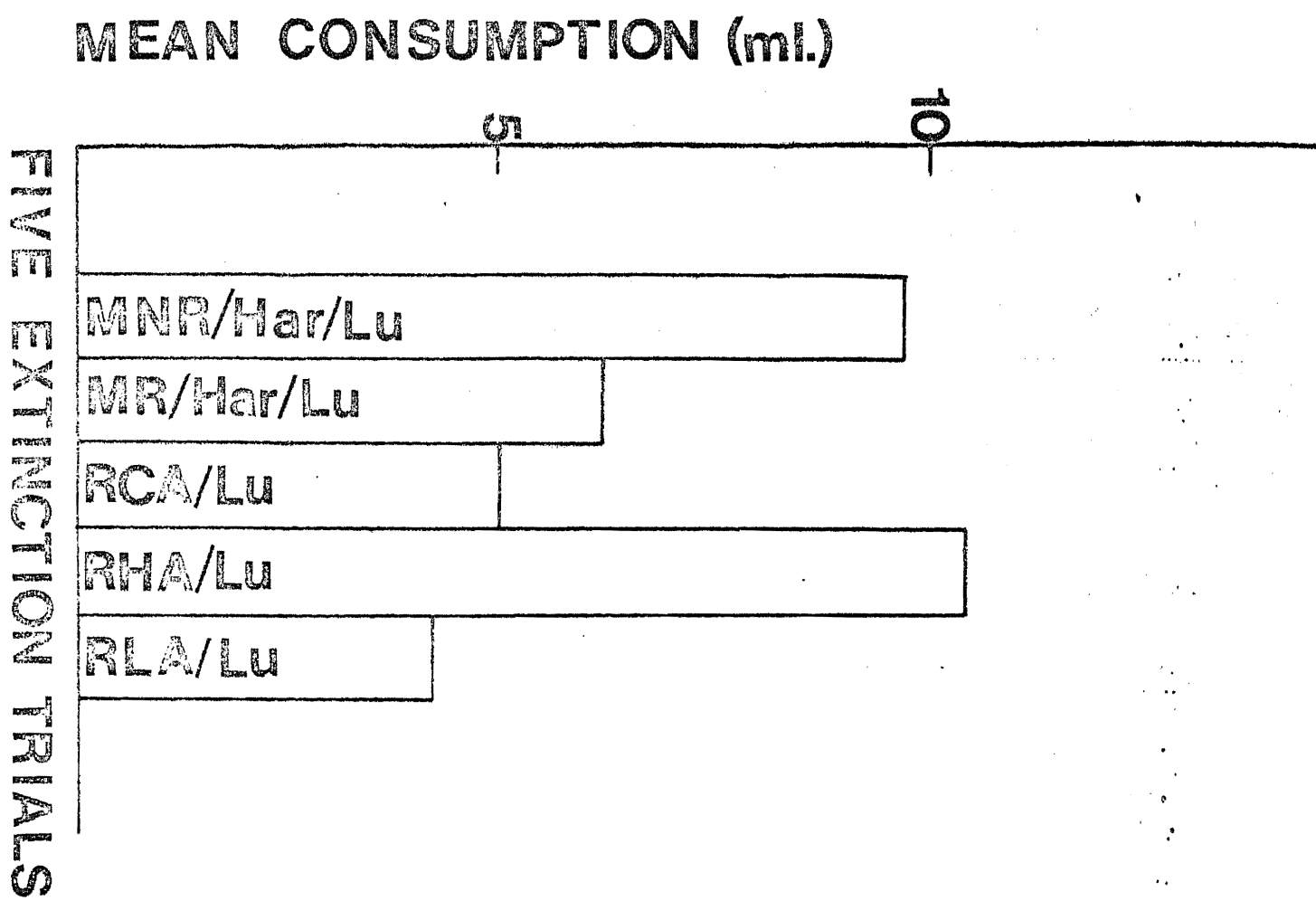
The MNR/Har/Lu, MR/Har/Lu, RCA/Lu and RHA/Lu strains consumed significantly more of the novel solution on conditioning trial 1 than familiar solution on Day 6 (see Table 4).

This suggests that there is a possibility at least for the four above strains that the novel solution was more preferred than the familiar solution. It should be pointed out, however, that during the familiar solution phase the mean consumption of distilled water for each strain increased each day and did not stabilize. Thus the higher consumption of novel solution on conditioning trial 1 may indicate a continuation of the unstablized pattern.

The mean volume of the liquids consumed during the five extinction days for all the strains of rats are presented in Figure 1. A strain was considered to have reached extinction if there was no significant difference between the amount of the novel solution consumed on the given extinction day and the amount consumed on conditioning trial 1.

The MNR/Har/Lu and RHA/Lu strains, which displayed the lowest magnitude of taste aversion learning, showed the highest degree of extinction learning compared to the MR/Har/Lu, RCA/Lu, and RLA/Lu strains (see Figure 3). Also, the MNR/Har/Lu and RHA/Lu were the only strains to reach extinction by fifth extinction trial (see Table 5). The RLA/Lu strain, which displayed the highest magnitude of taste aversion learning showed the lowest amount of extinction learning. Similarly, the MNR/Har/Lu strain, which exhibited the lowest magnitude of taste aversion conditioning displayed the highest magnitude of extinction learning. Thus the relationships that existed among the strains in terms of the magnitude of extinction learning were the same as the relationships among the strains

Figure 3: The mean volume of novel solution consumed for the five strains of rats over the five extinction trials for all groups.


MEAN CONSUMPTION (ml.)
5
10
FIVE EXTINCTION TRIALS
MNR/Har/Lu
MR/Har/Lu
RCA/Lu
RHA/Lu
RLA/Lu

T A B L E 5

ANALYSIS OF VARIANCE FOR ALL GROUPS OF RATS

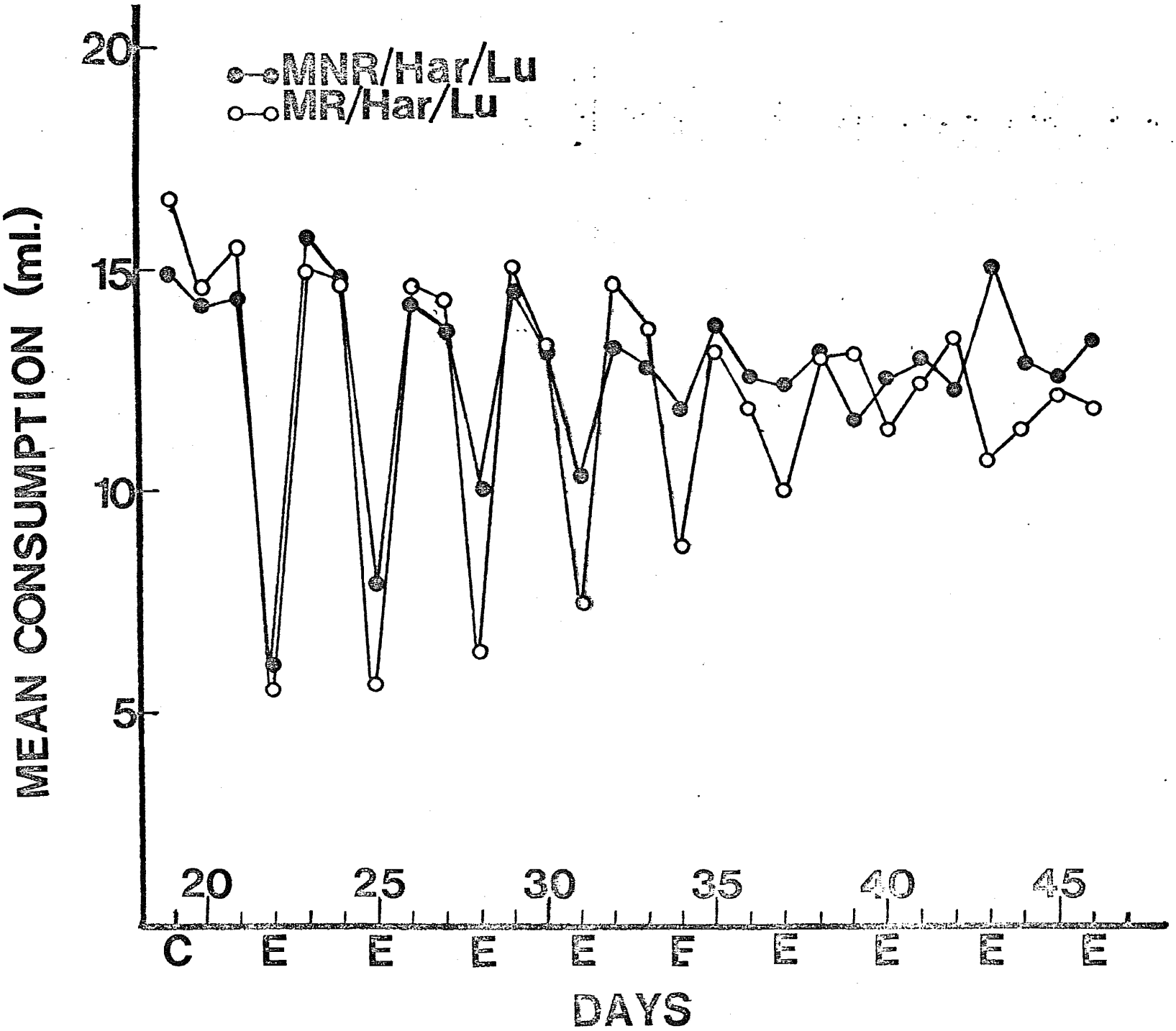
SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F ratio
Between conditioning trial 1 and extinction trial 1						
Sex	1,10	0.1	0.4	1.1	1.2	0.3
Trial	1,10	51.0*	45.3*	156.0*	87.5*	102.9*
Interaction	1,10	1.5	4.7	22.8*	2.3	7.1
Between conditioning trial 1 and extinction trial 2						
Sex	1,10	0.2	1.6	0.0	1.9	0.0
Trial	1,10	13.7*	40.6*	106.2*	40.7*	53.1*
Interaction	1,10	0.0	2.7	27.5*	1.2	5.3
Between conditioning trial 1 and extinction trial 3						
Sex	1,10	0.1	0.2	0.2	2.2	0.0
Trial	1,10	8.7	37.5*	76.6*	19.2*	49.0*
Interaction	1,10	0.0	5.7	16.7*	0.4	5.9
Between conditioning trial 1 and extinction trial 4						
Sex	1,10	0.7	1.4	0.1	8.3	0.2
Trial	1,10	10.9*	26.0*	54.5*	17.0*	29.4*
Interaction	1,10	0.1	2.6	13.8*	0.1	3.1
Between conditioning trial 1 and extinction trial 5						
sex	1,10	1.9	3.0	0.2	14.5*	0.5
Trial	1,10	5.0	21.6*	43.4*	2.0	18.5*
Interaction	1,10	0.6	2.0	12.6*	2.0	1.8

with the magnitude of taste aversion learning.

The results also indicate that for all of the strains faster extinction is related to slower learning. This is in accordance with the general finding in conditioning studies of an inverse relationship between the ease of acquisition and extinction (Kimble, 1961). This inverse relationship was also found in the avoidance conditioning of the MNR and MR strains (Owen, 1963).

The mean volume of the liquids consumed during the nine extinction days for all the strains of rats in Groups B and C are presented in Figure 4. It appears that only some of the strain differences during acquisition persisted over the nine extinction trials. The MNR/Har/Lu and RHA/Lu strains showed a higher magnitude of extinction learning than the MR/Har/Lu, RLA/Lu and RCA/Lu strains (see Figure 5) and extinguished two trials earlier than any of the other strains (see Table 6). The MNR/Har/Lu and RHA/Lu strains had displayed the lowest magnitude of taste aversion learning. The RHA/Lu strain was close to the MNR/Har/Lu strain in displaying the lowest amount of taste aversion learning and was superior to all the strains including the MNR/Har/Lu strain in extinction learning. It should be pointed out, however, that this strain reached extinction at the same time as the RLA/Lu and MR/Har/Lu strains (i.e. by extinction trial 4). The RLA/Lu strain which showed the highest taste aversion learning was close to the RCA/Lu and MR/Har/Lu strains in displaying lower extinction learning.

Figure 4 and Figure 4a: The mean volume of the liquids consumed for the five strains of rats each day during the nine extinction trials of Experiment 1 for groups B and C. Among the data points plotted is the first conditioning trial (C), on day 7, followed by the nine extinction trials (E) on days 22, 25, 28, 31, 34, 37, 40, 43, and 46.


MNR/Har/Lu
MR/Har/Lu
MEAN CONSUMPTION (ml.)
20
15
10
5
20
25
30
35
40
45
C
E
E
E
E
E
E
E
E
E
DAYS

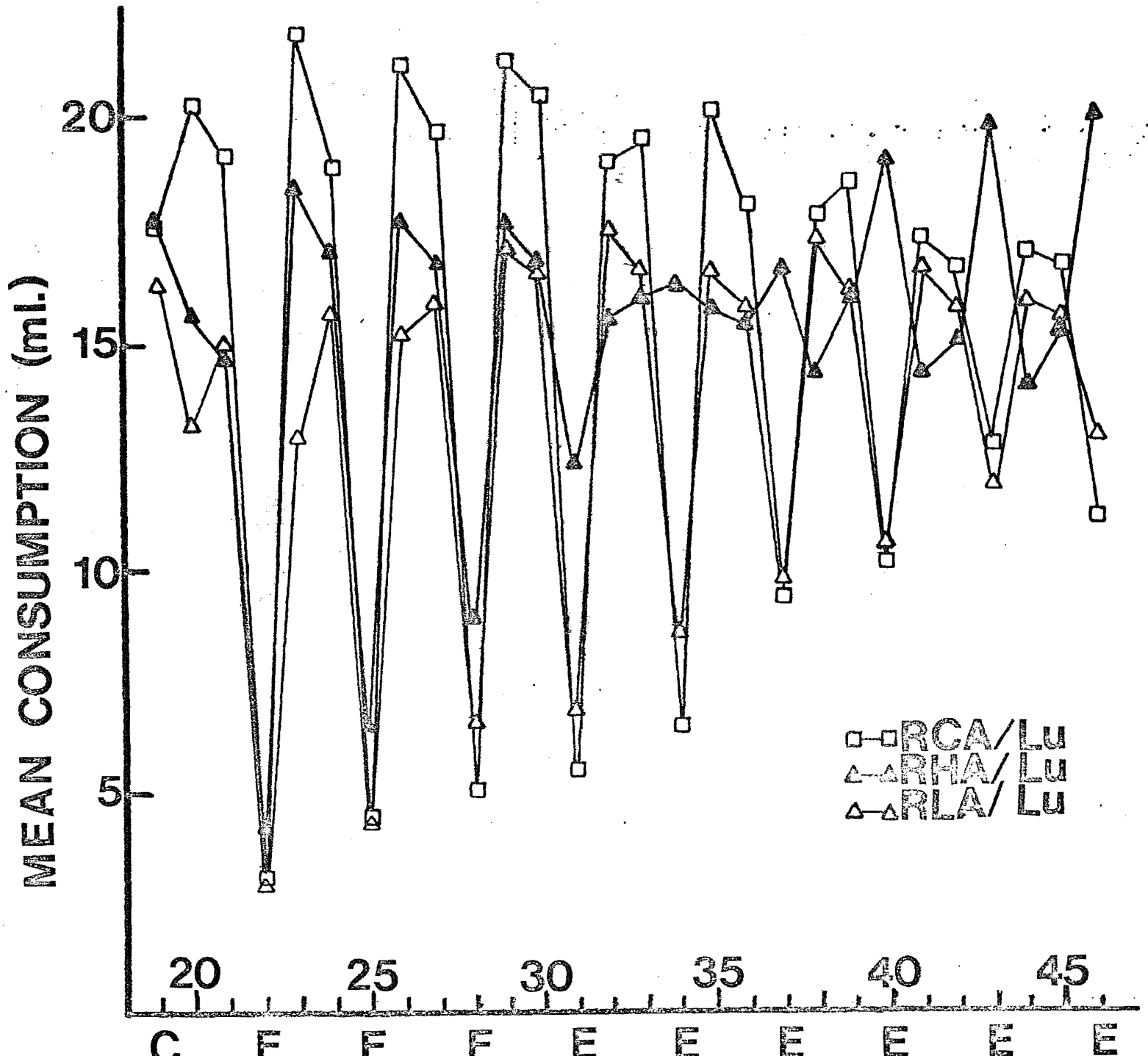

MEAN CONSUMPTION (ml.)
20
15
10
5
20
25
30
35
40
45
RCA/Lu
RHA/Lu
RLA/Lu

Figure 5: The mean volume of novel solution consumed for the five strains of rats over the nine extinction trials for all groups.

MEAN CONSUMPTION (ml.)
5
10
MINE EXTINCTION TRIALS
MNR/Har/Lu
MR/Har/Lu
RCA/Lu
RHA/Lu
RLA/Lu

TABLE 6

ANALYSIS OF VARIANCE FOR GROUPS B AND C

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F ratio
Between conditioning trial 1 and extinction trial 1						
Sex	1,6	0.0	0.2	0.4	5.7	0.1
Trial	1,6	33.6*	19.1*	84.3*	85.8*	51.5*
Interaction	1,6	0.4	1.1	13.6	2.9	7.1
Between conditioning trial 1 and extinction trial 2						
Sex	1,6	0.5	1.1	0.0	0.6	0.1
Trial	1,6	10.5	19.5*	48.0*	32.1*	24.2*
Interaction	1,6	0.2	0.4	13.4	3.1	5.2
Between conditioning trial 1 and extinction trial 3						
Sex	1,6	0.6	0.4	0.2	3.4	0.0
Trial	1,6	5.5	17.8*	35.5*	27.7*	20.7*
Interaction	1,6	0.2	1.1	7.7	1.2	4.5
Between conditioning trial 1 and extinction trial 4						
Sex	1,6	1.5	1.9	0.1	5.1	0.4
Trial	1,6	5.7	13.3	21.3*	8.5	11.0
Interaction	1,6	0.7	0.2	5.0	0.0	2.0
Between conditioning trial 1 and extinction trial 5						
Sex	1,6	1.7	4.3	0.5	9.9	1.4
Trial	1,6	2.7	14.0*	23.5	0.7	6.5
Interaction	1,6	0.7	0.0	5.0	0.7	0.9

TABLE 6

ANALYSIS OF VARIANCE FOR GROUPS B AND C

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F ratio
Between conditioning trial 1 and extinction trial 6						
Sex	1,6	2.2	5.8	1.0	21.4*	3.0
Trial	1,6	1.7	7.7	8.8	0.3	5.5
Interaction	1,6	1.1	0.0	1.4	0.3	0.4
Between conditioning trial 1 and extinction trial 7						
Sex	1,6	2.7	11.7	0.4	7.4	2.4
Trial	1,6	2.5	4.8	8.0	1.9	5.0
Interaction	1,6	1.1	0.1	3.2	0.0	0.7
Between conditioning trial 1 and extinction trial 8						
Sex	1,6	7.1	19.3*	1.0	31.0*	1.8
Trial	1,6	0.0	10.2	7.1	3.5	3.5
Interaction	1,6	2.9	0.1	4.5	6.5	0.7
Between conditioning trial 1 and extinction trial 9						
Sex	1,6	8.6	9.7	0.6	12.6	3.7
Trial	1,6	5.8	5.3	11.4	2.2	2.5
Interaction	1,6	2.3	0.4	5.5	1.4	0.6

* $p < .01$.

Thus it appears again that there is a relationship between faster extinction and slower learning among the MNR/Har/Lu, RHA/Lu, RCA/Lu, and MR/Har/Lu strains.

The differences among the strains during the five extinction trials were more like the strain differences during acquisition than were the strain differences over the nine extinction trials. However, it should be pointed out that these results could have been obscured by ceiling effects. That is, there was a smaller difference between some of the strains over the nine extinction trials due to the fact that some of the strains had reached complete extinction and were displaying the maximum magnitude of extinction learning. It seems unlikely that these results were caused by differences between Groups B and C, and Group A since, as mentioned earlier, there were no significant differences between these groups.

There were significant sex differences and sex by trial interactions in intake of novel and familiar solutions during both aquisition and extinction (see Tables 1 to 7). When the significant sex differences occurred the males consumed more fluid than the females of the respective strains but for the following exception: both sexes of the MR/Har/Lu strain consumed the same amount of fluid on the first familiar solution day and on the third and fourth conditioning trials. The strains which showed significant sex differences for absolute body weight were not similiar to the strains which showed significant sex differences when the results were corrected for body weight. This suggests that the significant sex differ-

TABLE 7

ANALYSIS OF VARIANCE FOR ALL GROUPS

SOURCE	df	MNR/Har/Lu F ratio	MR/Har/Lu F ratio	RCA/Lu F ratio	RHA/Lu F ratio	RLA/Lu F ratio
Over days 1 to 6						
Sex	1,10	1.7	14.8*	9.8	17.3*	0.4
Trial	1,10	12.0*	20.7*	13.0*	22.9*	45.1*
Interaction	1,10	0.7	3.6	1.3	0.9	0.7

* $p < .01$.

ences in consumption were due to body weight differences between the sexes. Thus perhaps the males consumed more fluid since they weighed more than the females of the respective strains.

Studies using these strains to investigate the voluntary consumption of alcohol have found sex differences in consumption. (Satinder 1972, 1975). Satinder (1972) found that the female rats drank significantly more absolute alcohol per gram of body weight than the males, however, there were no significant sex differences based on the actual amounts of alcohol irrespective of body weight differences and proportions of alcohol solutions. Satinder explained that the observed sex differences based on corrected body weight consumption do not seem to be related to biological differences but rather to differences in body weight. In a more recent investigation Satinder (1975) determined that there were significant genotype - dependent sex differences in the consumption of lower concentrations of alcohol when the body weight differences were obvious. Thus sex differences in consumption appeared to be primarily due to differences in body weight.

The MR/Har/Lu strain was the only strain that showed significant sex differences when the first conditioning trial was compared to the test trials. The significant differences occurred on the first three test trials. Both sexes displayed the same magnitude of taste aversion learning on the second and third test trials. It also appears that the sex differences for the MR/Har/Lu strain on the first test trial did

not occur as a result of conditioning since these differences existed prior to conditioning (i.e. over the six-day familiar solution phase). This strain did not show significant sex differences during extinction except for the comparison of conditioning trial 1 with extinction trial 8 (for Groups B and C).

As discussed earlier in the paper the symptoms of the lithium chloride induced illness that were established in the pilot study and measured in this investigation included: (1) the rats' eyes less than half open, (2) the rats lying down with their heads down, and (3) diarrhea. The illness period for both the .4M and .7M LiCl lasted approximately 75 minutes.

The results for each of the symptoms are presented in Tables 8 and 9. There were no significant differences for the symptoms of "eyes less than half open" and "lying down with head down" comparing the interval of time when the illness should have been present (i.e. on conditioning trial 2) with time intervals when it should have been absent (i.e. on Days 9 and 11). Thus it appears that these symptoms are not sensitive enough measures for this experiment. This is not surprising since rats are nocturnal animals and could be expected to have their eyes less than half open and to be lying down with their heads down for lengthy periods of time during the day regardless of whether or not they are sick.

There were significant differences between two non-illness periods (i.e. on Days 9 and 11) for the symptoms of "eyes less than half open" and "lying down with head down".

TABLE 8

ANALYSIS OF VARIANCE FOR ALL GROUPS OF RATS

SOURCE	df	Symptom: Eyes Less Than Half Open F ratio	Symptom: Lying Down With Head Down F ratio	Symptom: Diarrhea F ratio
On conditioning trial 1				
Strain	4,50	1.9	1.8	11.0*
Sex	1,50	1.3	3.5	0.1
Interaction	4,50	0.7	1.6	4.2*
Between conditioning trial 1 and conditioning trial 2				
Strain	4,50	2.4	3.8*	16.5*
Sex	1,50	1.4	13.8*	0.8
Interaction	4,50	2.1	2.2	10.4*
Trial	1,50	23.2*	4.9	11.0*
Trial X Strain interaction	4,50	2.3	1.7	6.0*
Trial X Sex Interaction	1,50	0.0	3.0	0.1
Trial X Strain X Sex Interaction	4,50	1.3	0.3	1.9

TABLE 9

ANALYSIS OF VARIANCE FOR GROUP A

SOURCE	df	Symptom: Eyes Less Than Half Open F ratio	Symptom: Lying Down With Head Down F ratio	Symptom: Diarrhea F ratio
Between conditioning trial 2 and day 9				
Strain	4,10	2.5	0.3	5.0
Sex	1,10	7.4	11.1*	1.0
Interaction	4,10	1.3	2.5	11.0*
Trial	1,10	0.1	0.0	25.0*
Trial X Strain Interaction	4,10	2.1	2.3	5.0
Trial X Sex Interaction	1,10	0.1	1.4	1.0
Trial X Strain X Sex Interaction	4,10	0.7	1.9	11.0*
Between conditioning trial 2 and day 11				
Strain	4,10	0.6	0.7	5.0
Sex	1,10	2.6	5.1	1.0
Interaction	4,10	2.8	4.0	11.0*
Trial	1,10	7.2	5.7	25.0*
Trial X Strain Interaction	4,10	2.6	1.3	5.0
Trial X Sex Interaction	1,10	0.0	0.8	1.0
Trial X Strain X Sex Interaction	4,10	0.9	0.4	11.0*
Between day 9 and day 11				
Strain	4,10	0.6	0.5	0.0
Sex	1,10	1.9	5.5	0.0
Interaction	4,10	0.8	2.1	0.0
Trial	1,10	10.1*	10.1*	0.0
Trial X Strain Interaction	4,10	2.3	1.9	0.0
Trial X Sex Interaction	1,10	0.1	5.6	0.0
Trial X Strain X Sex Interaction	4,10	2.3	0.8	0.0

This provides further evidence to indicate that this symptom may not be a sensitive enough measure for this experiment since if there was still some presence of illness on the first recovery day (Day 11) and if this was significantly less than on the day before the injection was given, then it would follow that there should be a significant difference in the occurrence of these symptoms between the conditioning trial and the day before the conditioning trial.

The results indicate that the symptom of "diarrhea" is a sensitive enough measure to detect the presence or absence of LiCl induced illness for the MNR/Har/Lu, MR/Har/Lu, and RLA/Lu strains. These strains showed the presence of this symptom on the second conditioning trial and the absence of this symptom on the day before and after conditioning trial 2 (i.e. on Days 9 and 11). The RCA/Lu and RHA/Lu did not display this symptom on any of these days. The results indicate that there was no direct relationship among the strains between the occurrence of the symptoms of "diarrhea" and "eyes less than half open" and the magnitude of taste aversion learning. For the symptom of "lying down with head down" there was a direct relationship for the MNR/Har/Lu, MR/Har/Lu, RCA/Lu, and RHA/Lu strains between its occurrence during the illness period on conditioning trial 1 and the magnitude of taste aversion learning on conditioning trial 2, and for the RCA/Lu and RHA/Lu strains between the occurrence of the symptom during the illness period on conditioning trial 2 and the degree of taste aversion learning on conditioning trial 3.

In view of the fact that this direct relationship was not found for the symptoms of "eyes less than half open" and "diarrhea", and for most of the strains on the second conditioning day for the symptom of "lying down with head down", it must be concluded that it does not seem probable that differences in the strains' sensitivity to the UCS could account for the observed strain differences in taste aversion learning. However, it should be pointed out that only one of the three symptoms ("diarrhea") appeared to be a sensitive enough measure for this experiment. Thus further investigations with more reliable measures is necessary before any conclusions can be reached.

As reported earlier, the MR/Har/Lu strain was the only strain that displayed signficant sex differences in taste aversion learning. There appears to be no relationship in terms of significant sex differences for the MR/Har/Lu strain between the occurrence of any of the symptoms and the magnitude of taste aversion learning. Thus the results suggest that the sex differences were not due to differences in sensitivity to the UCS.

It appears that there is no evidence to support a classical conditioning model of taste aversion learning. There were no symptoms elicited by the presentation of the

CS during the drinking periods on the first three conditioning trials and on the fourth test trial (or on any of the recovery days in between the first four conditioning trials). Also only a small proportion of the animals (i.e. four out of the twenty animals, three of which were from the MR/Har/Lu strain) showed the symptoms on the third test day. The symptoms displayed on the third test day did not include the symptom of "diarrhea" which was found to be the most sensitive measure for this experiment. (On the last familiar solution day three animals showed some occurrence for either the symptoms of "eyes less than half open" or "lying down with head down.)

EXPERIMENT 2

The purpose of this experiment was a control study. It should be pointed out that on the basis of earlier research it appears that a control group is not essential in this study. Many studies (for example, Brackbill, Rosenbush and Brookshire, 1971; Hargrave and Bolles, 1971) have found that

the amount of novel substance consumed by the drug-injected rats was markedly less than the amount consumed by the saline injected controls. Also the control groups consumed the same amount of the novel and familiar solutions after the saline injections as they did before injection.

It is possible that some of the strains of rats are more sensitive than others to any pain caused by the injection. However, any pain that is caused by the injection should not produce a taste aversion since, as mentioned earlier in the paper, rats will maintain or increase their consumption of a novel fluid if it has been paired with a painful stimulus such as electrocutaneous shock (Garcia et al 1972; Green et al., 1972).

METHOD:

Experimental Design:

This experiment compares the amount of conditioned taste aversion among the five strains of rats to a novel solution when followed by an injection of 6 ml./kg. of a solution of .4 molar lithium chloride with the amount of conditioned taste aversion to the same novel solution when followed by an injection of 6 ml/kg. of distilled water. All the rats in Group A were used for this experiment after the termination

of Experiment 1. Since not all of the rats had fully extinguished by the end of Experiment 1 further extinction days were given until all the animals showed no evidence of taste aversion learning. At the end of Experiment 1 the animals were given a 20 minute access to distilled water on day 1 followed by 3 extinction trials within the same paradigm of Experiment 1 with the exception that on the second extinction day the rats were allowed a 24 hour access to the novel solution. By the third extinction trial there was no indication of taste aversion learning for any of the strains.

Subjects:

The subjects were the 20 rats in Group A that were used in Experiment 1. There were 4 from MNR/Har/Lu, MR/Har/Lu, RHA/Lu, RLA/Lu, and RCA/Lu strains, equally represented by sex. The experimental design was a 5 x 2 factorial design. There was one male and one female from each strain in the experimental and in the control groups. All the rats were reared and maintained under the conditions reported in Experiment 1.

Apparatus:

The apparatus set up was the same as reported in Experiment 1.

Procedure:

The experimental paradigm consisted of two phases: the conditioning phase and testing phase. The conditioning phase took place on days 1, 4 and 7. The testing phase took place on days 4, 7 and 10. On each of these days the rats were weighed and then allowed a 20 minute access to a bottle of the

novel solution at the same time each day. The amount of fluid consumed was recorded. On each day, with the exception of day 10, 45 minutes after the drinking period, half of the rats from each strain received injection of 6 ml/kg. of .4 M lithium chloride (experimental group) and the other half of the animals received an injection of 6 ml./kg. of distilled water (control group). Following each of the conditioning trials and/or testing trials the rats were allowed two recovery days with a 20 minute access to a bottle of the familiar solution. On day 10 the procedure was the same as it was on a conditioning trial except without the UCS.

Results:

The following measures were obtained from each animal: (a) the amount of familiar solution consumed each day during the familiar solution phase and on the recovery days; and (b) the amount of novel solution consumed each day during the conditioning and testing phases. All the results were evaluated by an analysis of variance. The only differences that were considered significant were those with associated probabilities less than .01.

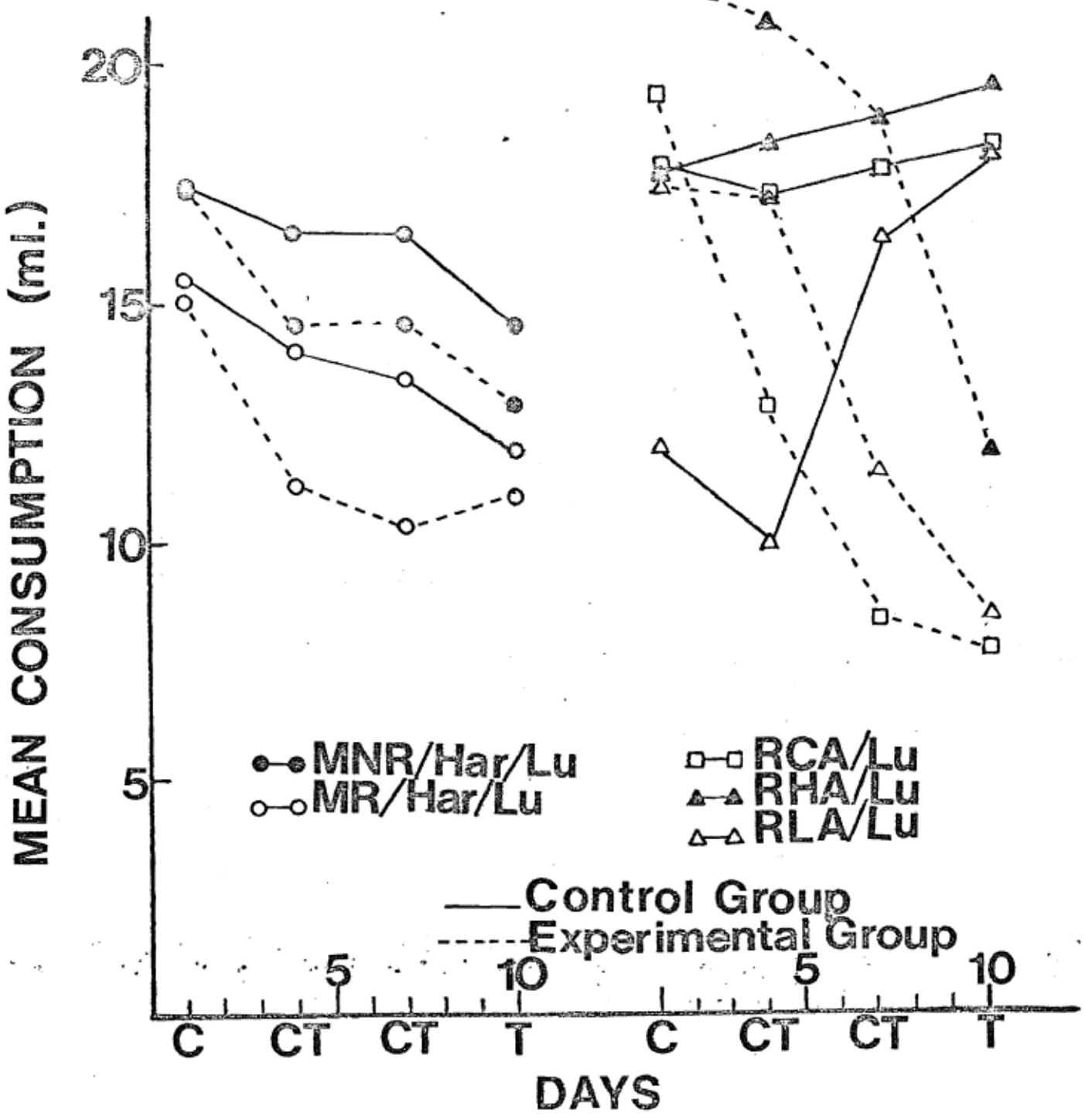
All comparisons were made for absolute body weight. There were no significant differences between the control and experimental groups over all four test trials. However, there was a significant difference for trials alone ($F = 5.66$, $df = 3/30$, $p < .01$) and there was a significant trials by groups interaction ($F = 6.81$, $df. = 3/30$, $p < .01$).

The amount of novel solution consumed by the drug injected groups of the RCA/Lu, RHA/Lu, and RLA/Lu was less than the distilled water injected groups by the third test day (see Figure 6). Also the control groups of the RCA/Lu and RHA/Lu strains consumed the same amount of novel solution after the distilled water injections as before the injections. The control group of the RLA/Lu strain consumed even more of the novel solution on the last two test days than before the injections. Thus the results for the RCA/Lu, RHA/Lu, and RLA/Lu strains supports the evidence that it was the association with the toxicosis rather than the pain of the injection which caused the taste aversion learning. This also supports the evidence that aversions to familiar flavours can be obtained if no other relevant stimulus is available (Garcia and Koelling, 1967). It should be pointed out, however, that the control and treatment groups of the MNR/Har/Lu and MR/Har/Lu strains consumed nearly the same amount of novel solution on each test trial, and consumed less novel solution on each of the test trials than on conditioning trial 1.

The reason why there was no significant difference between the control and treatment groups over all three test trials was probably due to the fact that the animals had learned over the previous extinction trials that the sugar solution was safe, and also because the sugar solution was now very familiar to them. Aversions to flavours are less pronounced if the flavours are familiar than if they are novel (Farley et al, 1964; Garcia

and Koelling, 1967; McLaurin et al, 1963; Revusky and Bedarf, 1967). Thus more than three acquisition trials would be necessary for taste aversion learning to occur for all the strains.

Figure 6: The mean volume of the liquids consumed for the five strains of rats during each day of Experiment 2 for both the experimental and control groups. The data points plotted consist of the first conditioning (C) trial on day 1, two conditioning and test trials (CT) on days 4 and 7, and one test trial (T) on day 10.


MEAN CONSUMPTION (ml.)
20
15
10
5
MNR/Har/Lu
MR/Har/Lu
RCA/Lu
RHA/Lu
RLA/Lu
Control Group
Experimental Group
5
10
5
10
C
CT
CT
T
C
CT
CT
T
DAYS

GENERAL DISCUSSION

The results indicate that strain differences exist in taste aversion learning. The RLA/Lu and MR/Har/Lu strains were superior in taste aversion learning compared to the RHA/Lu and MNR/Har/Lu strains. The RCA/Lu was intermediate between the RLA/Lu and RHA/Lu strains in the magnitude of taste aversion learning. The RLA/Lu strain displayed the highest magnitude of taste aversion learning compared to the other five strains and the MNR/Har/Lu strain showed the lowest degree of taste aversion learning.

The findings clearly demonstrate that the differences between the strains which were genetically selected for the behavior of high and low rates of avoidance conditioning were not generalizable to taste aversion learning. The relationship between the RLA/Lu and RHA/Lu strains, and between the MNR/Har/Lu and MR/Har/Lu strains in terms of the magnitude of taste aversion learning was the inverse of the relationship for the learning ability in avoidance conditioning. Similarly, the learning ability in avoidance conditioning and taste aversion conditioning was inversely related between the RHA/Lu and MNR/Har/Lu strains, and the RLA/Lu and MR/Har/Lu strains. These results differed from Dragoin's (1971) study which found a direct relationship between avoidance learning and taste aversion learning using the Long Evans hooded and the Sprague-Dawley albino strains. However, it should be pointed out that the question of strain differences in Dragoin's study is equivocal since the two strains of rats were procured from different commercial sources. Although further research

is needed, the present findings suggest that avoidance conditionability is not among the mechanisms which regulate taste aversion learning.

There are several tentative hypothesis regarding the mechanisms or components of taste aversion learning which could have been modified in different genotypes. Perhaps the genetic differences in taste aversion learning rates of the five strains are due to differences in taste preference for the CS among the strains. A number of studies have shown that the magnitude of taste aversion learning varies according to taste preference for the CS. However, there exists conflicting evidence as to whether there is, in fact, greater taste aversion for the most preferred or least preferred substance (Green and Churchill, 1970; Sutker, 1971; Kalat and Rozin, 1970). Thus if there were strain differences in taste preference it is not clear in what direction it would affect the magnitude of taste aversion learning.

The novel solution used in the present investigation was shown to be a highly preferred substance for each of the five strains. A pilot study by Satinder (1973) showed that each of the strains displayed more than a 60% preference for the 5% sugar solution compared to less than 30% for 2.5% and less than 3% for 1.25% sugar solutions. In the present investigation it appears that the MNR/Har/Lu, MR/Har/Lu, RHA/Lu, and RCA/Lu strains did not differ in taste preference among themselves and showed a higher preference for the novel solution than the RLA/Lu strain. Thus the differences in taste aversion

learning among the MNR/Har/Lu, MR/Har/Lu, RHA/Lu, and RCA/Lu strains were not due to differences in taste preference. It seems unlikely that the RLA/Lu strain's lower preference for the CS caused the high magnitude of taste aversion learning for this strain since the other strains which did not differ in taste preference did display differences in taste aversion learning. However, in order to determine if differences in the taste aversion learning rates between the RLA/Lu strain and the other strains are due at least in part to the differences in taste preferences, it would be necessary to equate the taste preference of RLA/Lu strain with the other strains by varying the concentration of the sugar solution, and then compare the magnitude of taste aversion learning among these strains.

Recent studies have demonstrated that the strength of a rat's aversion to saccharin is a direct function of the amount of saccharin it consumed prior to poisoning (Bond and DiGiusto, 1975). In this investigation, the MNR/Har/Lu, MR/Har/Lu RHA/Lu, and RCA/Lu strains did not differ by much in the amount of the CS consumed prior to poisoning. Thus the genetic differences in taste aversion learning rates of these strains are not due to differences in CS consumption. The RLA/Lu strain which was superior in taste aversion learning consumed less of the novel solution prior to poisoning. This result cannot be considered to conflict with the findings that the strength of aversion varies directly with amount of CS consumed before conditioning since the comparison was made with

different strains. That is, the possibility exists that there are other mechanisms or components of taste aversion learning that are modified in different genotypes which could account for the observed strain differences. In addition, it seems unlikely that differences between the RLA/Lu strain and the other strains in taste aversion learning was due to the RLA/Lu strain's lower consumption of the CS prior to conditioning since the other strains displayed differences in taste aversion learning even though they did not show differences in the CS consumption. To determine if the genetic differences in taste aversion learning rates between the RLA/Lu and the other strains is due to differential consumption of the CS, an experiment would have to be conducted in which the five strains consume a given equal amount of the CS before conditioning.

Many researchers have reported that the magnitude of learned aversions increases with the severity of the UCS (Garcia et al., 1967; Revusky, 1968; Dragoin, 1971; Wright et al., 1971; Nachman and Ashe, 1973). Thus it could be possible that the RLA/Lu, RCA/Lu and MR/Har/Lu strains are more sensitive to the unconditioned effects of the LiCl induced illness than are the MNR/Har/Lu and RHA/Lu strains. The evidence from this study indicates that there is no direct relationship among the strains between the occurrance of the symptoms during the illness period on each conditioning trial and the magnitude of taste aversion learning on the following test trials. Thus it does not seem probable that differences

in the strains' sensitivity to the UCS could account for the observed strain difference in taste aversion learning. However, it should be pointed out that as discussed earlier, only one of the three symptoms ("diarrhea") appeared to be a sensitive enough measure for this experiment. Thus further investigations with more reliable measures which could perhaps include symptoms, such as, heart rate and rectal temperature is necessary before any conclusions can be reached. If it is found that there are genetic differences among the five strains of rats in sensitivity to the unconditioned effects of the induced illness, then equivalent states of aversive motivation as UCS levels should be used to determine if motivational differences among these strains of rats are the determinants of taste aversion learning.

Learned aversions have more frequently been compared procedurally to classical conditioning than to operant conditioning (Garcia and Ervin, 1968; Zahorik and Maier, 1969). In terms of the effects of both CS and UCS intensity, many studies indicate that taste aversion learning (Dragoin, 1971; Garcia et al, 1967; Revusky, 1968; Wright et al, 1971) is similar to classical conditioning (Beecroft, 1955; Kimble, 1961; Razran, 1957). The present investigation found no evidence to support a classical conditioning model of taste aversion learning. After one or more pairings, the presentation of the CS did not elicit some of the symptoms of the illness (CR). However, further investigations which measure more reliable symptoms are necessary before any definitive

conclusions can be reached. In a study with thiamine deficiency no equivocal evidence was found for the presence of conditioned responses to both the tastes paired with recovery and the tastes paired with deficiency (Zahorik, 1972).

Perhaps a comparison between taste aversion behavior and avoidance behavior might provide some insight into the possible mechanisms for the observed strain differences in taste aversion behavior. It seems clear that taste aversion conditioning could be described as a passive type of learning while one-way and two-way active avoidance conditioning is clearly an active type of learning. Thus it is possible that increased general activity could indirectly produce superior performance in active avoidance conditioning and have little effect in taste aversion learning. However, as mentioned earlier genetic differences in avoidance learning rates of the RHA/Lu and RLA/Lu strains are not due to differences in general activity among these strains (Satinder and Hill, 1974). It has not been determined if the differences in avoidance learning for the MNR and MR strains could be due to the increased general activity of the MNR strain. The motivation differences due to differential shock sensitivity do not explain entirely the strain differences in avoidance conditioning for the RHA/Lu and RLA/Lu strains (Satinder and Petryshyn, 1974) and there are no differences in foot-shock sensitivity for the MNR/Har/Lu and MR/Har/Lu strains (Wilcock, 1968; Satinder, 1976).

Satinder and Petryshyn (1974) determined that it is possible that the differences in avoidance learning are partly due to the differences in the level of arousal in the RHA/Lu and RLA/Lu strains. They point out that "information from the two-way and one-way active avoidance behaviour and its modification by d-amphetamine provide reasonably convincing evidence to propose that RHA/Lu and RLA/Lu strains differ on a inverted - U Shape arousal function." The authors explain that this is due to the fact that the one-way task is less complex in nature than the two-way task (Anisman, 1973; Anisman and Waller, 1972; Ashe and McCain, 1972; Theios and Dunaway, 1964) and on these two tasks the avoidance performance of these strains indicate that RHA/Lu has a relatively high level of arousal compared with the RLA/Lu strain. It seems reasonable to expect that an organism with a low level of arousal will have a poor performance on a complex task compared with an organism with a relatively higher level of arousal, and for a simple task the organism with a low level of arousal has a better performance than on a complex task. Also if the organism with the low and high levels of arousal are induced to higher levels of arousal then the organism with the initial low level of arousal will improve in performance on complex and simple tasks, and the organism with the initial high level of arousal will either deteriorate or show a plateau in performance on complex and simple tasks. This does represent the performance of the RLA/Lu and RHA/Lu strains

respectively, under the effects of d-amphetamine in both two-way and one-way avoidance tasks (Satinder and Petryshyn, 1974).

Perhaps the genetic differences in taste aversion learning are due to differences in the level of arousal in the RHA/Lu and RLA/Lu strains. It appears that taste aversion learning, a passive type of learning, is less complex in nature than the one-way active avoidance task. It seems reasonable to believe that an organism with a low level of arousal would have a better performance on the simpler taste aversion learning task compared with an organism with a relatively higher level of arousal. This describes the performance of the RLA/Lu and RHA/Lu strains in the taste aversion task. To determine if these strain differences in taste aversion learning are due to differences in arousal level the strain with the lower level of arousal would have to be induced to a higher level of arousal and its performance measured once again on taste aversion learning. For example, the RLA/Lu strain could be injected with increasingly higher doses of d-amphetamine in separate experiments prior to the drinking periods on the conditioning and testing days. If the differences in taste aversion learning are due to differences in arousal level then the strain with the initial low level of arousal will either deteriorate or show a plateau in the performance curve.

As of yet there has been no investigation to determine if MNR/Har/Lu strain, which is superior to the MR/Har/Lu strain in avoidance conditioning, has a higher level of arousal than

the MR/Har/Lu strain. However, it is possible that the same proposed relationship of taste aversion learning and avoidance conditioning with arousal level may exist for these strains.

There appears to be a relationship between taste aversion learning and the phenotype of emotional reactivity since the strain with a high open-field defecation score (MR/Har/Lu) showed greater taste aversion learning than the strain with a low score (MNR/Har/Lu). This suggest that emotional reactivity may be among the mechanisms which regulate the magnitude of taste aversion learning.

The genetic differences in taste aversion learning of the MNR/Har/Lu and MR/Har/Lu strains do not appear to be due to differences in "intelligence" or conditionability among the strains. There have been varied results in the conditioning studies using the MR and MNR strains (Garg and Holland 1967, 1968, and 1969; Garg 1970; Imada 1972; Weldon 1968).

In taste aversion learning some chemical stimuli (gustatory, olfactory) have a high associative strength relative to the consequence of toxicosis. (Barnett, 1953; Garcia and Koelling, 1967). Perhaps the genetic differences in taste aversion learning among the MNR/Har/Lu, MR/Har/Lu, RHA/Lu and RLA/Lu strains are due to differential sensitivity to the gustatory or olfactory cue.

It is also possible that the hypothesized central mechanism underlying taste aversion learning has been differentially modified by the various breeding programs that produced these

strains. Research in this area could help determine the mechanism which mediates long-interval taste aversion learning.

In this investigation significant sex differences and sex by trial interactions in consumption of novel and familiar solutions occurred during both acquisition and extinction. However, it appears that the differences in intake were primarily due to body weight differences between the sexes since when the results were corrected for body weight the sex differences for these strains disappeared. Similar to this, previous investigations using these strains have found that sex differences in the voluntary consumption of alcohol appeared to be primarily due to differences in body weight. (Satinder 1972, 1975). As suggested by Satinder in reference to the voluntary consumption of alcohol, the best way to determine whether the sex differences in intake are due to biological differences other than body weight would be to study the intake "in sexually mature animals of both sexes, of the same age, with natural physical development but not differing significantly in body weight. This could be achieved by genetic selection in which females are bred for higher body weight and males for lower body weight." (Satinder 1975, P. 1505).

The MR/Har/Lu strain was the only strain that showed any significant sex differences in taste aversion learning. However, it also appears that the sex differences did not occur as a result of conditioning since these differences existed prior to conditioning (i.e. over the six-day Familiar Solution Phase).

In conditioning studies there is generally an inverse relationship between the ease of acquisition and extinction (Kimble, 1961). This inverse relationship was also found in the avoidance conditioning of the MNR and MR strains (Owen, 1963). The results with the MNR/Har/Lu, MR/Har/Lu, RHA/Lu RLA/Lu and RCA/Lu strains in the present investigation support these findings.

A P P E N D I X 1

SYMPTOM RECORDING SHEET

NIMAL NO.									
ying down ith head own									
yes less han half pen									
yes half pen									
Eyes more han half pen									
Jnable to bserve eyes									
Defecation nard									
Defecation soft									
Defecation runny									
Animal No.									

DATE:

TIME OF OBSERVATIONS:

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