CONDITIONED FOOD AVERSIONS: ILLNESS-INDUCED AVERSIONS TO THE INTERACTION OF GUSTATORY AND NONGUSTATORY CUES

By

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ABSTRACT

Laboratory rats were habituated to drinking sucrose in one environment (the sucrose environment) and water in a second (the water environment). Subjects poisoned after drinking sucrose in the water environment subsequently exhibited a marked reduction in sucrose intake in the water environment. The same subjects did not exhibit depression of water consumption in the water environment and showed only a slight, nonsignificant reduction of sucrose intake in the sucrose environment. These results indicate that rats will form an aversion to a compound stimulus consisting of both gustatory and environmental components without forming an aversion to either the gustatory or environmental component in isolation.

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INTRODUCTION

Both wild and laboratory rats are hesitant to ingest novel foods and consume only limited amounts of distinctively flavored substances the first time they are experienced. With repeated exposure to a taste the amount consumed is gradually increased unless ingestion of that taste has undesirable consequences. If experience of a novel flavor is followed by malaise, foods of that flavor will subsequently be avoided (Barnett, 1963; Chitty, 1954; Rzoska, 1953). A conditioned aversion to a flavor can be established after only one or two pairings of that flavor with toxicosis and such aversions may be learned even if the taste experience is separated from the aversive drug treatment by more than an hour (for reviews, see Garcia & Ervin, 1968; Garcia, Hankins & Rusiniak, 1974).

Aversions are readily acquired only to novel tastes. If there has been extensive preexposure to a flavor prior to its pairing with illness, aversion is absent (Revusky & Bedarf, 1967; Siegel, 1974).

Historically, gustatory stimuli have proven to be the cues which rats most easily associate with illness. Garcia and Koelling (1966) compared the relative strengths of aversions acquired to a taste and to a combined light-noise stimulus, both of which had been paired with toxicosis. A taste and an audiovisual cue (a light flash and clicking noise) were made contingent on licking at a drinking spout. When consumption of bright-noisy-tasty water was followed by illness, rats showed strong aversions to the taste cue but exhibited no aversion to the audiovisual cue. This difference in the relative associability of the audiovisual and taste cues with toxicosis was not due to the relative salience of the two stimuli. If, instead of toxicosis, footshock was made consequent upon ingestion, aversions were formed solely to the audiovisual cue. The results of this experiment led the authors to suggest that rats have a genetically based predisposition to associate illness with interoceptive cues and not to associate illness with exteroceptive cues.

The impact of Garcia and Koelling's (1966) finding is evidenced by the fact that subsequent research in toxicosis aversion learning has been focused on gustatory cues, to such an extent that the general area of investigation has been termed taste aversion learning. Nevertheless, a number of studies have demonstrated that rats can acquire aversions to nongustatory stimuli when these have been paired with toxicosis. For example, it has been shown that rats will readily associate olfactory cues with toxicosis (Domjan, 1973; Garcia & Ervin, 1968; Lorden, Kenfield & Braun, 1970) and can do so despite a temporal delay in the onset of illness, comparable to that tolerated in taste aversion conditioning (Rudy & Cheatle, in press; Taukulis, 1974). Rats also learn to avoid thermal or tactile stimulation to the tongue paired with illness and do so in spite of a 15-min delay intervening between stimulation and toxicosis onset (Nachman, 1970; Nachman, Rauschenberger & Ashe, 1977). Furthermore, rats will learn to reject distinctive visual stimuli which have accompanied a novel tasting food prior to toxicosis induction (Galef & Osborne, 1978; Morrison & Collyer, 1974) as well as visual cues which have been presented in the absence of edibles (Best, Best & Mickley, 1973; Garcia, Kimeldorf & Hunt, 1956).

In the natural environment a potential toxin would often be accompanied by visual, olfactory, tactile, and other nongustatory cues as well as by a taste cue. As mentioned above, it has been argued that in situations in which illness is paired with a food having both gustatory and nongustatory attributes, rats will acquire an aversion primarily to the taste (Garcia & Hankins, 1977; Hankins, Rusiniak & Garcia, 1976). However, failure to make use of the visual and olfactory attributes of toxic food objects would result in energy wasted in procuring and tasting foods which have previously caused illness, foods which are rejected once they are tasted (Galef & Osborne, 1978). Second, because a variety of cues can be used to identify a toxic food object, the animal which can learn to associate illness only with taste cues has an unnecessarily limited ability to discriminate toxic foods from safe ones. Although most toxins common in nature have a bitter taste, not all bitter tasting substances are toxic. An aversion directed at the taste cue alone would be transferred to all foods of similar taste, causing the rat to reject foods which are safe. Taking advantage of the nongustatory cues which distinguish nutritious edibles from toxic ingesta would enhance the rats' capacity to discriminate one from the other.

The present experiment was undertaken to determine whether aversions may be acquired to food objects, a food object being defined by a combination of both gustatory and nongustatory components. According to this model, any novel eating-related cue will label the ingested substance as a novel food object and will allow it to be readily associated with illness (Galef & Osborne, 1978; Rozin & Kalat, 1971; Testa & Ternes, 1977). In addition, an aversion is learned, not to the taste alone, but rather to the combination of gustatory and nongustatory cues specifying the food object. If this second view is correct, then rats should be able to readily learn an aversion to a food object which is a novel combination of familiar cues. In particular, rats habituated to both a distinctive taste and to a set of nongustatory cues should readily learn to avoid the novel joint occurrence of taste and nongustatory environment when this combination is paired with illness.

The aim was, therefore, to show that rats can readily learn to avoid the novel combination of a familiar taste and a familiar environment when their joint occurrence is followed by toxicosis. The procedure involved the use of two distinctive containers, each positioned in a discriminable environment. In the initial Habituation Phase of the experiment all animals were habituated to drinking sucrose in one environment (the sucrose environment) and to drinking water in a second environment (the water environment). During the Conditioning Phase which followed, the experimental subjects were presented with sucrose in the water environment and were then injected with a toxin. Control subjects received an identical injection following water ingestion in their home cages. Finally, three tests were administered to each subject, designed to assess the degree of aversion to 1) sucrose in the sucrose environment, 2) water in the water environment, and 3) sucrose in the water environment. An aversion to the interaction of the taste of sucrose with the water environment would be demonstrated if the experimental subjects drink significantly less sucrose than control subjects in the water environment while the two groups did not differ significantly in intake in the familiar combinations of sucrose in the sucrose environment and water in the water environment. If an aversion to the combination of the taste of sucrose with the nongustatory cues provided by the water environment can be acquired independently of any aversion to the taste, then the aversion must have been learned, not to the taste, but to the food object which is a combination of taste and nongustatory cues.

METHOD

Subjects and Maintenance

Twenty-four male Long-Evans rats averaging 204g at the time of the initiation of the experiment, obtained from Canadian Breeding Farms, St. Constant, Quebec, served as subjects. Each subject was housed individually in a 24x19x17 cm standard steel hanging cage with Purina Lab Chow available ad lib. Throughout the experiment water in the home cage was provided in a lidded glass jar 6.5 cm high and 5.5 cm in diameter, with a 3 cm round opening cut in the lid, through which the subject drank. Four days prior to the initiation of the experiment, each subject was placed on a 1 hr/day drinking schedule.

Apparatus

The apparatus consisted of two drinking compartments. Compartment A was a small plywood box, 20x20x20 cm with a clear Plexiglas ceiling and a plywood floor covered with Beta chips. A 100-ml plastic drinking tube fitted with a rubber stopper and steel spout was mounted on Compartment A so that the spout entered the box through a hole drilled 4 cm from the floor. Compartment B was a standard white plastic cage, 36x31x16 cm, with a grid top. It contained a 8x10x7 cm rectangular glass dish, placed on the bare cage floor.

Procedure

Each subject was randomly assigned to one of two groups which differed in the condition under which they received injections of toxin. During the Habituation Phase, which lasted for 20 days, all subjects were habituated to drinking 10% sucrose solution in one environment (a subject's "sucrose environment") and to drinking water in a second environment (a subject's "water environment").

On Day 1 of the experiment subjects were allowed a 30 minute drinking period in their sucrose environment where 10% sucrose solution was available in the container. They were then returned to their home cages for a half hour access to water. On Day 2 they were exposed for 30 minutes to water in the water environment, followed again by a half hour of water in their home cages. This two day sequence was repeated 10 times during the Habituation Phase.

The Conditioning Phase started on Day 21. On this day experimental subjects experienced a 30 minute drinking period involving the novel combination of sucrose in the water environment. Immediately thereafter, the subjects were taken to a separate room and injected intraperitoneally with .15M LiCl (20ml/kg). Control subjects received a similar injection following a 30 minute period of access to water in their home cages. Following the injection, all subjects were returned to their home cages for the usual half hour drinking period. On Days 23, 31 and 33 the conditioning treatment was repeated. Experimental subjects, therefore, received a total of four exposures to sucrose in the water environment, each followed by a toxic injection. Since control subjects were poisoned after drinking water in their home cages they never experienced sucrose in the water environment prior to the final test.

Between conditioning days, on Days 25 to 30 and again on Days 35 to 40, each subject was rehabituated to drinking sucrose in its sucrose environment and water in its water environment.

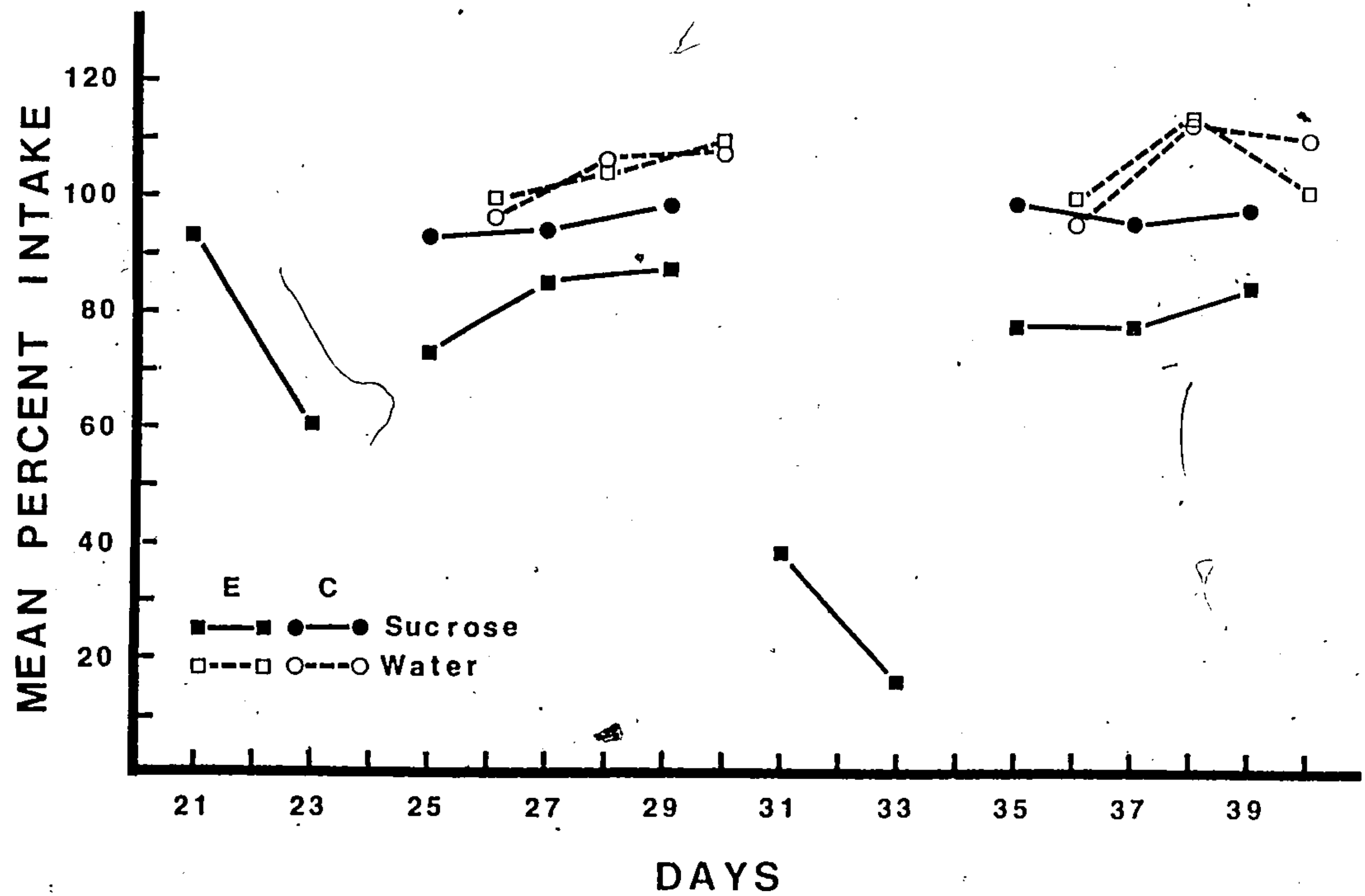
During the Test Phase, a 30 minute test was administered to each subject on three consecutive days. Total fluid intake was recorded for each subject when drinking 1) sucrose in the sucrose environment, 2) water in the water environment, and 3) sucrose in the water environment. Each 30 minute test was followed by 30 minutes access to water in the home cage. The order of presentation of the three tests was varied across subjects so that each possible order was represented in each group.

RESULTS

Figure 1 shows the mean fluid intakes of control and experimental subjects during the Conditioning Phase of the experiment. Fluid intakes presented in Figure 1 are expressed as percentages of the amount consumed by each subject on its final day of habituation, which was Day 19 in the case of sucrose and Day 20 in the case of water. On Days 21, 23, 31, and 33 experimental subjects drank sucrose in the water environment and were subsequently poisoned. The graph shows a sharp decrease in consumption over these four days. On the same days control subjects were injected after drinking water in their home cages. Excessive spillage from the glass jars used as water containers in the home cages prevented accurate recording of the intakes of control animals on these days.

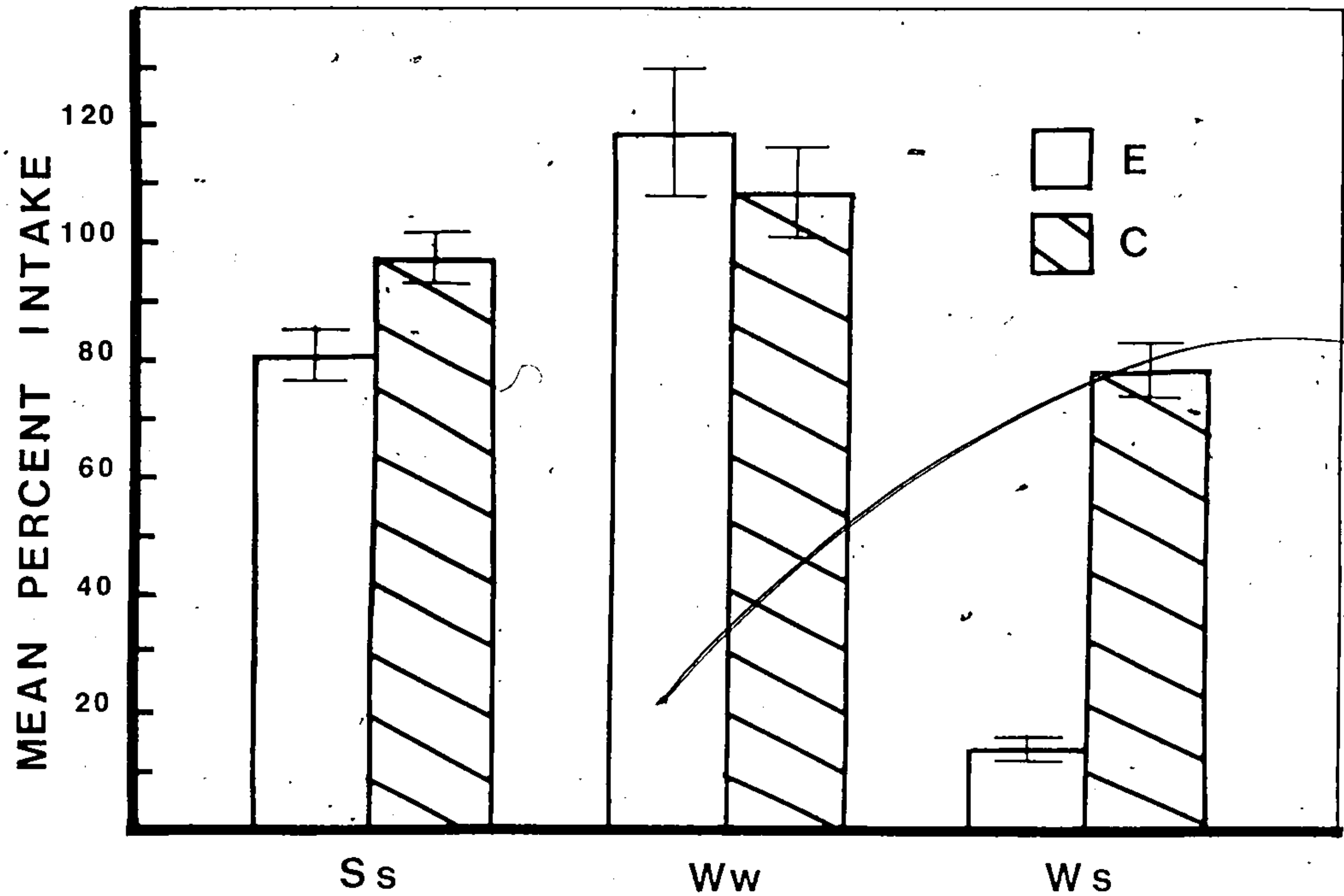
Results from the final Test Phase of the experiment are presented in Figure 2. Fluid intakes of the experimental and control subjects have again been expressed as percentages of the intakes on the last days of the Habituation Phase. As is clear from inspection of the figure, experimental subjects show a substantial aversion to the poisoned combination of sucrose in the water environment. A two-way analysis of variance on the amount consumed on the final three tests revealed a significant overall difference between experimental and control subjects, $\underline{F}(1,22) = 53.65$, $\underline{p} < .001$. There was also a significant Treatment X Test interaction, $\underline{F}(2,44) = 35.90$, $\underline{p} < .001$. A Scheffe

Figure 1: Mean fluid intakes of control and experimental subjects during the Conditioning Phase. Fluid intakes are expressed as percentages of the amount consumed by each subject on its final day of habituation which was Day 19 in the case of sucrose and Day 20 in the case of water. (Abbreviations: E=Experimental Group; C=Control Group)



MEAN PERCENT INTAKE
120
100
80
60
40
20
21
23
25
27
29
31
33
35
37
39
DAYS
E
C
Sucrose
Water

Figure 2: Mean fluid intakes of control and experimental subjects during the Test Phase. Fluid intakes are expressed as percentages of the amount consumed by each subject on its final day of habituation which was Day 19 in the case of sucrose and Day 20 in the case of water. (Brackets represent standard errors of the means. Abbreviations: E=Experimental Group; C=Control Group; Ss=Sucrose in the Sucrose Environment; Ww=Water in the Water Environment; Ws=Sucrose in the Water Environment)


MEAN PERCENT INTAKE
120
100
80
60
40
20
E
C
Ss
Ww
Ws

Test for Multiple Comparisons was undertaken to determine the source of the main effect of Treatment. Comparisons of the means of the experimental and control groups indicate a significant difference in intake of sucrose in the water environment ($p < .001$) but a nonsignficant difference in intake of sucrose in the sucrose environment and in water intake in the water environment ($ps > .05$).

DISCUSSION

The suppression of consumption exhibited by experimental subjects when drinking sucrose in the water environment cannot be accounted for either by an aversion to sucrose alone, an aversion to the water environment alone, or by the additive effects of the two. If animals that rejected sucrose in the water environment had been avoiding only the taste of sucrose, then intake of sucrose in the sucrose environment would have decreased to the same extent as intake of sucrose in the water environment (see Figure 2). If the aversion was directed toward the water environment then subjects would have rejected water in the water environment. To the contrary, test results indicated that experimental and control subjects drank approximately equal amounts of water in the water environment. The experimental animals acquired an aversion to the combination of sucrose taste in the water environment.

The presentation of sucrose in the water environment can be viewed as a compound CS made up of two components, the sucrose taste and the nongustatory cues provided by the water environment. Wagner and Rescorla (1972) assumed a compound stimulus to be made up of three parts, the two stimuli, A and B, and a third configural cue, AB, produced by the joint occurrence of A and B. Conditioning to a configural cue was found to be a slow process requiring a very large number of trials (Rescorla, 1972; Saavedra, 1975; Whitlow & Wagner, 1972). In the present experiment an aversion was rapidly acquired to the combination of two components, the sucrose taste and the water environment. Experimental subjects tested after four training trials drank an average of only 3 ml during the 30 minute test. There are many procedural differences between the present experiment and traditional configural cue conditioning experiments which might account for the relative speed with which aversions are formed to the interaction of taste and ingestive environment. One factor which may be important in the case of a compound made up of taste and container is that both components are attributes of a single object. Traditional experiments dealing with conditioning to configural cues have used discrete stimuli emanating from disparate points in space. It is possible that the joint occurrence of two stimuli is a more salient cue when these stimuli have a similar spatial location.

It has been found repeatedly in the past that rats can associate an illness experience with a novel taste after only one taste-illness pairing. The speed with which this kind of association is formed means that it is a type of learning which is likely to be a significant factor in the determination of food habits in the natural habitat. The results of the present experiment show that rats can readily associate illness with the interaction of taste and other eating-related cues. The readiness with which these animals learned an aversion to a food object, independent of any aversion to its taste, makes it likely that this ability makes a significant contribution to the animals' survival in the wild by enhancing the capacity to discriminate toxic from safe ingesta.

There remains a question as to which of the many stimuli arising from the complex of container and compartment are important for an aversion to be formed to the interaction of taste and environment. One stimulus which is likely to play a part in the present study is tactile stimulation of the tongue. Such stimulation occurs when the tongue makes contact with the solution and container during the licking movement (Nachman et al., 1977). Afferents coming from the mechanical receptors in the tongue, like those from the taste receptors, are projected onto the solitary nucleus, although they most probably connect to a different region (Blomquist & Antem, 1965). Rats will readily associate tactile-tongue stimulation with illness (Nachman et al., 1977) and it may well be the most salient cue provided by a fluid container.

Finally, the proposal that rats acquire food aversions primarily to taste cues has as a corollary that food aversions are independent of context (Hankins, Rusiniak & Garcia, 1976). If the avoidance response is directed only at the taste of food then that taste will be rejected to the same degree independent of changes in the outward appearance of the food or in the environment in which it is located. Although there has been some evidence of taste aversion transfer (Garcia, Kovner & Green, 1970; Gillette, Bellingham & Martin, 1979), these experiments have involved procedures in which the subjects have had experience with the nongustatory contextual cues prior to training and these cues are therefore very nonsalient relative to the novel taste. In the present experiment the animals in the experimental group demonstrated a very strong aversion to the sucrose taste in the water environment but drank significantly more sucrose in the sucrose environment, thus demonstrating an undeniable effect of context.

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