

**DEMONSTRATOR QUALITY AND SOCIAL TRANSMISSION OF FOOD
PREFERENCE**

THE INFLUENCE OF DEMONSTRATOR QUALITY ON
THE SOCIAL TRANSMISSION OF FOOD PREFERENCE
IN THE NORWAY RAT (*Rattus norvegicus*)

By

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ABSTRACT

An observer rat that interacts with a conspecific, a demonstrator that has eaten a flavoured food, is subsequently more likely to eat that food than an alternative, novel food (Galef & Wigmore, 1983). In the first part of this thesis, four experiments were undertaken to determine the influence of unreliable demonstrators on observer food preference. In the first three experiments, observers were poisoned after interaction with demonstrators; a demonstrator that demonstrated a food that led to poisoning was considered an unreliable demonstrator. The first experiment compared the influence of an unreliable demonstrator and an unfamiliar demonstrator on observers' food preferences. Experiment 2 compared the influence of demonstration from an unreliable conspecific and a familiar conspecific that had only provided irrelevant information. The third experiment compared the influence of an unreliable and a reliable demonstrator. Experiment 4 compared the influence for protein-deficient observers of a demonstrator that had previously demonstrated a protein-deficient diet and a demonstrator that was unfamiliar. None of the first four experiments showed a significant difference in effectiveness of social transmission due to demonstrator quality.

In the second part of the thesis I investigated the influence of familiarity on demonstrator effectiveness. In Experiment 5, the influence of local sisters was compared

with that of unfamiliar non-relatives as demonstrators. Sisters were not better demonstrators than unfamiliar non-relatives.

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GENERAL INTRODUCTION

When a rat ingests a flavoured food and interacts with a conspecific that has never seen that flavoured food, the conspecific that has never seen that flavoured food is significantly more likely to eat that food than another novel food. The original eater of the food, the demonstrator, conveys signals about the food eaten to another conspecific, the observer. Observers then prefer the food demonstrated; this effect is robust across a wide variety of experimental manipulations (e.g. Galef, Kennett, & Wigmore, 1984).

An exhaustive study of the influence of particular demonstrators on social transmission of food preference has not been undertaken, but a few experiments make suggestions about the role of individual demonstrators. For example, it has been shown that weanling rats pay more attention to adult demonstrators than to age-mate conspecifics (Gerrish & Alberts, 1995). However, it has been shown that cues from mother to weanling are no more effective than if the mother is replaced by an unfamiliar conspecific (Leon & Moltz, 1971). Conspecifics can also be a powerful contextual force for the development of food preferences; food aversions can disappear upon interaction with a conspecific that ate a food that had previously been aversive for an observer (Galef, McQuoid & Whiskin, 1990; Galef, 1985). Although these studies and others (Galef, et al., 1984) hint at the importance of particular demonstrators, no direct investigation of the relevance of demonstrator reliability has been pursued.

Social transmission of food preference likely exists to provide security in food selection. If an individual has eaten a particular diet and survived without illness, it is probably safer to eat that diet than one of the many other illness or death-inducing novel diets in the foraging environment. However, all subjects may not equally benefit from socially acquired information. If there is variance, rats that do not attend to demonstrators may be riskier foragers, which would mean that some rats pay less attention to conspecifics than others. If it is true that any particular rat is a riskier forager, it might benefit that rat's conspecifics to ignore its messages about what foods are safe to eat. Additionally, Norway rats live in colonies of various sizes (Barnett, 1975). Large colonies may have more population flux; thus a resident of a large colony may frequently encounter conspecifics that are unfamiliar with a foraging area and thus potentially risky foragers.

Previous studies in this laboratory have shown that protein-deficient rats pay more attention to demonstration than protein-replete rats (Galef, Beck, and Whiskin, 1991). It has been hypothesized that this occurs because of the increased need on the part of protein-deficient observers for good dietary information (Galef, 1991). If observers have an increased need for good dietary information, they may also have an increased need to identify senders of bad dietary information. A demonstrator that has not demonstrated a food that helped an observer overcome its dietary inadequacy might be remembered as a bad demonstrator by a protein-deficient observer.

EXPERIMENT 1

In the first experiment, I tested a rat's ability to discriminate against conspecifics that provide unreliable information about novel foods. All observers received 3 days of demonstration, and on the first 2 days all observers were allowed to eat the food demonstrated for an hour and were then injected with a lithium chloride solution that made them ill. Observers were divided into two groups for the 3 days of demonstration. One group of observers saw a different demonstrator on each day of demonstration. The second group of observers saw the same demonstrator on each day of demonstration. After three demonstrations, observers were offered a choice between the food demonstrated (Diet Cin) and a novel food (Diet Coc). It was hypothesized that observers with the same demonstrator on the three days of testing would be biased against the conspecific that had provided unreliable information leading to poisoning the first 2 days. Thus I expected an observer that had Diet Cin demonstrated by a novel conspecific on the third day of demonstration would be more likely to eat Diet Cin than an observer that had Diet Cin demonstrated by a familiar but unreliable conspecific.

Method

Subjects

Twelve female, 42-day-old, Long-Evans rats (*Rattus norvegicus*), born in the McMaster University Vivarium, served as observers. Each observer was housed

individually in an 18 cm high x 18 cm wide x 34 cm deep wire mesh hanging cage. 12 additional female, 49-56 day-old, Long-Evans rats served as demonstrators. Each demonstrator was housed individually in an 18 cm high x 18 cm wide x 34 cm deep cage in a room separate from the observers, except during the 30 min of interaction between a demonstrator and its observer, when each demonstrator was placed in an observer's cage.

Half the demonstrators were assigned to the "Same Demonstrator" (Same Dem) group of observers and the remainder were assigned to the "Different Demonstrator" (Dif Dem) group of observers. The second and third time an observer in the Dif Dem group saw an unfamiliar demonstrator, that demonstrator had previously demonstrated for another observer in the Dif Dem group.

Foods

Four foods were composed by mixing powdered Purina Rodent Laboratory Chow #5001 with either 1% McCormick's Fancy Ground Cinammon and 1% white sugar (Diet Cin), 2% Hershey's Pure Cocoa (Diet Coc), 1% bulk ground anise (Diet Ani), or 2% bulk ground marjoram (Diet Mar).

Procedure

Days 1-4 For the first 4 days of the experiment, observers and demonstrators were placed on feeding schedules. The 12 demonstrators were fed Purina Chow from 10:00 AM to 11:00 AM. The 12 observers were fed Purina Chow from 11:30 AM to 12:30 PM.

Day 5 Observers were weighed at 10:00 AM. Each demonstrator ate Diet Ani from 10:00 AM to 11:00 AM. From 11:00 AM to 11:30 AM, each demonstrator interacted with its assigned observer. Then, each observer ate Diet Ani from 11:30 AM to 12:30 PM. Finally, at 12:30 PM, each observer was injected with 1% by weight of 1% weight by volume of LiCl solution.

Day 6 Day 6 provided recovery for observers from possible detrimental effects of the previous day's poisoning. All demonstrators ate Purina Chow from 10:00 AM to 11:00 AM. All observers ate Purina Chow from 11:30 AM to 12:30 PM.

Day 7 The procedure on day 7 was the same as that on day 5 except that on day 7, all demonstrators ate Diet Mar from 10:00 AM to 11:00 AM. From 11:00 AM to 11:30 AM, each observer in the Same Dem group interacted with its demonstrator from day 5. Each observer in the Dif Dem group interacted with an unfamiliar demonstrator. From 11:30 AM to 12:30 PM, all observers ate Diet Mar. All other procedures were as described for day 5.

Day 8 The procedure for day 8 was the same as that on day 6.

Day 9 The procedure on day 9 was similar to that on days 5 and 7 except that: (1) all demonstrators ate Diet Cin from 10:00 AM to 11:00 AM, (2) each observer in the Same Dem group interacted with its demonstrator from days 5 and 7, (3) each observer in

the Dif Dem group interacted with an unfamiliar demonstrator, and (4) at 11:30 AM, all observers were offered a choice between Diet Cin and Diet Coc.

At 1, 3, 6, and 24 hours after the choice was offered, I weighed each observer's food cups containing Diet Cin and Diet Coc. Percent Diet Cin was determined by dividing the Diet Cin intake by the total intake of Diet Cin and Diet Coc. I compared the cumulative percent Diet Cin intake for the Same Dem and Dif Dem observers at each interval after the choice was offered. Furthermore, I compared the Percent Diet Cin for the two groups of observers for the time intervals 0-1 h, 1-3 h, 3-6 h, and 6-24 h.

Results and Discussion

A Mann-Whitney U test on percent Diet Cin ingested during the 24 h following interaction revealed that the Dif Dem group did not show an increased preference compared to the Same Dem group ($U=11$, ns). In fact, the groups tended to differ in the opposite direction to the prediction (Figure 1), and after 1 h there was a nearly significant greater preference for Diet Cin in the Same Dem group ($U=6$, $p<.10$). Results for other measured intervals were not significant in either direction (3 h: $U=13$, ns; 6 h: $U=10$, ns).

Insert Figure 1 about here

A split plot, repeated measures ANOVA was performed on the measured time intervals. A comparison of the Same Dem and Dif Dem groups revealed a nearly significant increase in preference for the Same Dem group $F(1,10)=4.57, p<0.10$. There was also a significant difference for all subjects in percent intake of Diet Cin across the measured time periods $F(5,50)=8.54, p<.01$ and a significant interaction between time periods and demonstrator condition $F(5,50)=2.40, p<.05$. See Figure 2 for non-cumulative intake over the observed time periods.

Insert Figure 2 about here

The non-significant result in the ANOVA comparison between Same Dem observers and Dif Dem observers was in the opposite direction of my hypothesis. The Same Dem observers were almost significantly more likely to attend to their unreliable demonstrators than the Dif Dem observers were likely to attend to their unfamiliar demonstrators. I had hypothesized that previous experience of unreliable demonstration would result in discrimination against the unreliable demonstrator. If anything, in Experiment 1, it was the unreliable demonstrator that tended to be more influential.

It is possible that there was no significant difference between the Same Dem and Dif Dem observers because there were not enough unreliable demonstrations to generate discrimination against unreliable demonstrators. However, Norway rats are neophobic

(Barnett, 1975). It is possible that observers in the Dif Dem group had a neophobic response to the new demonstrator on the second and third day of demonstration. Even though each demonstrator in the Same Dem group was empirically unreliable, each demonstrator was familiar. Experiment 2 added a second demonstrator for each observer, thus eliminating the possibility of a neophobic confound.

EXPERIMENT 2

In Experiment 1, there was a non-significant trend for the Same Dem group to eat more of the experimental food than the Dif Dem group in the first hour. This suggested the possibility that unreliable demonstration was better than no previous interaction. A conspecific who is a member of a local foraging group might make an occasional mistake and still be a generally good demonstrator.

In Experiment 2, each observer had two demonstrators. The first demonstrator ate a food that the observer later ate, after which the observer was injected with lithium chloride and made ill. The second demonstrator ate a food that was never seen by its observer. Since the two demonstrators would be equally familiar to the observer, I hypothesized that the second demonstrator would be a better demonstrator on the test day, as the second demonstrator had not demonstrated a food that made its observer ill. The demonstrator that had made its observer ill would be remembered as unreliable; its later information would be ignored.

Method

Subjects

Thirty-two, 42-day-old, female Long-Evans rats, born in the McMaster University vivarium, served as observers. Each observer was housed individually in a 19 cm wide x 16.5 cm high x 30 cm deep wire mesh hanging cage. 64 additional Long-Evans rats, ages

49-56 days, served as demonstrators. Each demonstrator was housed individually in an 18 cm high x 18 cm wide x 24 cm deep cage in a room separate from the observers, except during the 15 min of interaction between a demonstrator and its observer, when each demonstrator was placed in its observer's cage.

Foods

Seven foods were composed by mixing powdered Purina Rodent Laboratory Chow #5001 with either 1% McCormick's Fancy Ground Cinammon and 1% white sugar (Diet Cin), 2% Hershey's Pure Cocoa (Diet Coc), 1% bulk ground anise (Diet Ani), 2% bulk ground marjoram (Diet Mar), 0.7% bulk ground thyme (Diet Thy), 0.7% bulk ground rosemary (Diet Ros), or 0.7% bulk ground cardamon (Diet Car).

Procedure

All procedures in Experiment 2 were the same as procedures in Experiment 1, except for the changes noted below.

Day 5 Each observer had two demonstrators. One demonstrator, the "unreliable" demonstrator, ate a flavoured food that the observer ate following demonstration. The other demonstrator, the "irrelevant" demonstrator, ate a flavoured food the observer never saw. Each observer interacted with one of its two demonstrators between 11:00 AM and 11:15 AM. Each observer interacted with its other demonstrator between 11:15 AM and 11:30 AM. On day 5, the irrelevant demonstrator ate Diet Ros and the unreliable

demonstrator ate Diet Thy. Each observer ate Diet Thy between 11:30 AM and 12:30 PM and was subsequently injected with a 1% by weight solution of 1% wt/vol LiCl. Order of interaction with unreliable and irrelevant demonstrators was counterbalanced across observers.

Day 6 Day 6 provided recovery for possible detrimental effects of the previous day's poisoning. All observers ate Purina Chow from 11:30 AM to 12:30 PM. All demonstrators ate Purina Chow from 10:00 AM to 11:00 AM.

Day 7 The protocol for day 7 was the same as the day 5 protocol, except on day 7 the unreliable demonstrator ate Diet Mar and the irrelevant demonstrator ate Diet Ani. All observers ate Diet Mar.

Day 8 The protocol for day 8 was the same as that on day 6.

Day 9 The protocol for day 9 was similar to that on days 5 and 7 except that on day 9, each observer saw one of its two demonstrators. Half the observers interacted with a demonstrator that had eaten Diet Car and the rest with a demonstrator that had eaten Diet Cin. Observers were also equally divided between those interacting with an irrelevant or unreliable demonstrator that ate Diet Cin on day 9. Hence, the 32 observers were divided into four groups of eight: Diet Cin, irrelevant; Diet Cin, unreliable; Diet Car, irrelevant; Diet Car, unreliable. The order in which observers had interacted with unreliable and

irrelevant demonstrators on days 5 and 7 was counterbalanced in assigning demonstrators to groups.

After demonstration, observers were offered a choice between Diets Cin and Coc. Measurement was made of Diet Cin and Diet Coc intake at 24 h. Percent Diet Cin was calculated for each time interval by dividing the Diet Cin intake by the total intake of Diets Cin and Coc.

Results and Discussion

A 2 x 2 ANOVA was performed comparing the main effects of demonstrator quality and food demonstrated on percent Diet Cin ingested by observers. As has frequently been the case (Galef and Wigmore, 1983), I found a main effect of demonstrated diet on later intake of Diet Cin $F(1,28)=19.64$, $p<.0001$. I was not able to find an effect of demonstrator quality on later intake of Diet Cin $F(1,28)=0.075$, ns. There also was not a significant interaction between the variables $F(1,28)=0.654$, ns. See Figure 3.

Insert Figure 3 About Here

These results were not in the direction of my hypothesis that observers would discriminate against unreliable demonstrators. There was no significant effect of demonstrator quality. Even though in the present experiment the unreliable demonstrator

demonstrated a food that caused an observer illness, that demonstration was no worse than demonstration of a food that an observer never saw.

A demonstrator that demonstrates an irrelevant food may not be familiar with the foraging area. Thus, a demonstrator that is unfamiliar with a foraging area might not be a better demonstrator than a demonstrator that has provided unreliable information. An observer could discriminate against an unreliable demonstrator and also a demonstrator with irrelevant information in favour of a conspecific that provides reliable information. In Experiment 3, I investigated whether a demonstrator that provided reliable information was better than a demonstrator that provided unreliable information.

EXPERIMENT 3

The irrelevant demonstrator in Experiment 2 was replaced by a reliable demonstrator in Experiment 3. While the food that did not result in illness was never seen in Experiment 2, in Experiment 3 the food that did not result in illness was later safely ingested by each observer. Since familiarity and relevance of demonstration were controlled, I expected the reliable demonstrator to be a better demonstrator than the unreliable demonstrator on the final day of testing.

Method

Subjects

Sixteen 42-day-old, female, Long-Evans rats, born in the McMaster University vivarium, served as observers. Each observer was housed individually in a 19 cm wide x 16.5 cm high x 30 cm deep wire-mesh hanging cage. 32 additional female, Long-Evans rats, ages 49-56 days, served as demonstrators. Each demonstrator was housed individually in an 18 cm wide x 18 cm high x 24 cm deep cage in a room separate from the observers, except during the 15 min of interaction between a demonstrator and its observer, when each demonstrator was placed in its observer's cage.

Foods

Six foods were composed by mixing Purina Rodent Laboratory Chow with either 1% McCormick's Fancy Ground Cinammon and 1% white sugar (Diet Cin), 2% Hershey's Pure Cocoa (Diet Coc), 1% bulk ground anise (Diet Ani), 2% bulk ground marjoram (Diet Mar), 0.7% bulk ground thyme (Diet Thy), or 0.7% bulk ground rosemary (Diet Ros).

Procedure

The procedure for Experiment 3 resembled the procedure of Experiment 2, except that foods designated for the irrelevant demonstrators in Experiment 2 were eaten by reliable demonstrators in Experiment 3. Changes are noted below.

Day 6 While day 6 was a recovery day in Experiments 1 and 2, day 6 was a day of demonstration in Experiment 3. Each demonstrator ate the same food it had eaten on day 5. However, after demonstration, each observer ate the food it had not been given on day 5. For example, on day 5 all observers interacted with a demonstrator that ate Diet Ros and a demonstrator that ate Diet Thy. The observer then ate Diet Thy for 1 h. Next, each observer was made averse to Diet Thy following an illness-inducing injection of LiCl.

On day 6, each observer saw the same two foods from the same two demonstrators as on day 5. In Experiment 3, each observer ate Diet Ros on day 6 and was not poisoned after ingestion of Diet Ros.

Day 8 All observers interacted with the same two demonstrators that had eaten the same two foods they had eaten on day 7. Once again, of the two foods demonstrated, observers ingested the one they did not see on day 7. In this case, the food ingested by observers on day 8 was Diet Ani. As on day 6, observers were not poisoned after ingestion on day 8.

Day 9 On day 9 all observers had one demonstrator eat Diet Cin and one demonstrator eat Diet Coc. Half of the observers had demonstration of Diet Cin from a demonstrator that had previously demonstrated safe foods, the rest had demonstration of Diet Cin from a demonstrator that had previously demonstrated illness-inducing foods.

As in Experiments 1 and 2, the intake of Diet Cin was measured at 1, 3, 6, 24, 48 and 72 hours after the choice was offered. As in the first two experiments, percent Diet Cin was determined by calculating the amount of Diet Cin eaten and dividing that by the total amount of Diet Cin and Diet Coc eaten. Percent Diet Cin was compared for cumulative time periods as well as for the non-cumulative intervals of measurement.

Results and Discussion

A Mann-Whitney U test measured the difference in percent Diet Cin intake for the two groups over the cumulative measured intervals. There was no significant difference in any time interval.

Insert Figure 4 About Here

A split-plot, repeated measures ANOVA was performed on the total intake in each measured time intervals; observers whose previously-reliable demonstrator ate Diet Cin did not consistently eat more Diet Cin than observers whose previously-unreliable demonstrator ate Diet Cin $F(1,14)=0.809$, ns. There was also no significant difference for intake intervals $F(5,70)=1.41$, ns and no significant interaction $F(5,70)=1.14$, ns.

Insert Figure 5 About Here

Previously unreliable demonstration did not lead to any reduction of intake of Diet Cin. In this experiment I controlled for the possible confound of relevant demonstration, and I found no difference between the groups. Taken together, the first three experiments suggest that Norway rats do not discriminate against conspecifics that eat poisonous foods.

EXPERIMENT 4

Galef, Beck and Whiskin (1991) showed that protein-deficient observers show an increase in induced preference compared to protein-replete observers. That was a somewhat unusual finding, given the general robustness of the phenomenon of social transmission of food preference. In the Galef, Beck and Whiskin (1991) study, protein-deficient observers had an unpalatable nutmeg diet demonstrated and ate more of the nutmeg diet than did protein-replete observers when given a later choice between nutmeg and a palatable food. As Galef (1991) suggested, a protein-deficient observer may not be able to afford a mistake; thus, in spite of nutmeg's bad taste, the protein-deficient observer might eat it because demonstration establishes it as safe.

In Experiment 4, I asked whether protein-deficient observers would discriminate against an unreliable demonstrator. Since a protein-deficient observer may perish if it does not find a protein-replete diet, that observer may not be able to allow an occasional demonstration mistake from an unreliable demonstrator.

Method

Subjects

Twenty 42-day-old, female, Long-Evans rats, born in the McMaster University Vivarium, served as observers. Each observer was housed individually in a 19 cm wide x 16.5 cm high x 30 cm deep wire mesh hanging cage. 20 additional female, Long-Evans

rats, ages 49-56 days, served as demonstrators. Each demonstrator was housed individually in an 18 cm wide x 18 cm high x 24 cm deep cage in a room separate from the observers, except during the 30 min of interaction between a demonstrator and its observer, when each demonstrator was placed in its observer's cage.

Foods

Two foods were composed by mixing powdered Purina Rodent Laboratory Chow #5001 with either 1% McCormick's Fancy Ground Cinammon and 1% white sugar (Diet Cin), or 2% Hershey's Pure Cocoa (Diet Coc). Two more foods were composed by mixing protein-free basal mix and 6% by weight high protein casein with either 1% bulk ground anise (Diet Ani), or 2% bulk ground marjoram (Diet Mar). The protein-free basal mix and 6% by weight casein (Diet Bas) served as a basal diet for the first four days of the experiment.

Procedure

Days 1-5 All observers were maintained on ad lib access to Diet Bas. Demonstrators ate Purina Chow from 10:00 AM to 11:00 AM. On day 4, all observers were weighed to confirm that observers were losing weight as a result of maintenance on the protein deficient diet. All observers had lost at least 10 g of body weight.

Day 6 On day 6, each demonstrator ate marjoram-flavoured Purina Chow from 10:00 AM to 11:00 AM. From 11:00 AM to 11:30 AM, each observer interacted with a demonstrator. At 11:30 AM, all observers were offered ad lib access to Diet Mar.

Day 7 On day 7, demonstrators ate anise-flavoured Purina Chow from 10:00 AM to 11:00 AM. From 11:00 AM to 11:30 AM, each observer interacted with a demonstrator. Each observer in the "Unreliable Demonstrator" (Unrel Dem) group saw the demonstrator it saw on day 6. Each observer in the "Unfamiliar Demonstrator" (Unfam Dem) group saw an unfamiliar demonstrator. At 11:30 AM, all observers were offered ad-lib access to Diet Ani.

Day 8 All demonstrators ate Diet Cin from 10:00 AM to 11:00 AM. From 11:00 AM to 11:30 AM, each observer in the Unrel Dem group saw the same demonstrator it had seen on days 6 and 7. As with day 7, each observer in the Unfam Dem group saw an unfamiliar demonstrator. At 11:30 AM, all observers were offered a choice between Diet Coc and Diet Cin.

As in the first three experiments, measurements of intake were made at 1, 3, 6, and 24 hours after the choice began. As well, percent Diet Cin was determined as the ratio of Diet Cin ingested/Diet Cin and Diet Coc ingested.

Results and Discussion

A Mann-Whitney U test was performed comparing the percent Diet Cin eaten by observers in the Unrel Dem group and the Unfam Dem groups. After 24 h, there was no significant difference between the groups (Mann-Whitney, $U=50$, ns). There was also no significant difference between groups at any other interval measured.

Insert Figure 6 about here

The split-plot repeated measures ANOVA on Experiment 4 revealed no difference in intake for observers with familiar and unfamiliar demonstrators $F(1,18)=0.041$, ns.

In Experiment 4 there was an effect of time after ingestion $F(3,54)=6.90$, $p<0.01$ but no interaction $F(9,54)=0.11$, ns.

Insert Figure 7 about here

The lack of a significant difference between these two groups might mean, as suggested before, that not enough unreliable demonstrations had occurred for an individual in the Same Dem group to begin discriminating against its unreliable

demonstrator. As mentioned previously, Galef (1991) has suggested that nutritional deprivation may lead to an increased attendance to demonstration, as the need for good information about food is greater for the protein-deficient observer than for the protein-replete observer. That increased need for good information may explain Galef, Beck and Whiskin's (1991) finding that protein-deficient observers show a greater attendance to demonstration than protein-replete observers.

However, it may also be true that an observer's increased need for reliable demonstration due to protein inadequacy makes it more, and not less, likely to attend to an unreliable demonstrator. An observer in the Same Dem group may associate a demonstrator with previous unreliable demonstration. However, since death may be imminent if a protein-deficient observer does not solve its nutritional problems, later information from an unreliable demonstrator may be utilized. Even though a demonstrator is unreliable, it may provide reliable information consistently enough to make its later information better than possible death by individual foraging.

GENERAL DISCUSSION

The experiments in the first part of this thesis investigated whether there was an effect of demonstrator quality on the social transmission of food preferences.

Demonstrator quality was measured by either illness-inducing demonstrated food or nutritionally-inadequate demonstrated food. Neither measure of demonstrator quality had a significant effect on observer diet preference.

Previous work in this laboratory has shown that context is critical to the social transmission of food preference (Galef, Kennett and Stein, 1985). Neither the application of flavoured chow to the posterior of an anesthetized demonstrator nor the application of chow to the anterior of a recently-sacrificed demonstrator served to increase the preference of observers. Flavoured chow applied to the anterior of a surrogate similarly failed to increase observer diet preference. However, flavoured chow applied to the anterior of an anesthetized demonstrator did enhance subsequent preference of observers for the flavoured chow (Galef and Stein, 1985). Since social learning occurs in very specific contexts, one relevant context might be demonstrator quality. Although the experiments reported here do not show an effect of demonstrator quality, there may be circumstances not tested here that do influence the the effect of demonstrator quality on social transmission of food preference.

There are many potential ways that natural selection could have favoured the existence of observer attendance to demonstrator quality. As social transmission is a

dynamic process, some of these pressures are a function of the behaviour of demonstrators while others are a function of behaviour of observers.

Variance in attending to demonstration

In the basic transmission paradigm, a demonstrator eats a flavoured food and interacts with an observer; then, the observer has the opportunity to choose between the novel food the demonstrator ate and another novel food the demonstrator did not eat. While observers generally have a significantly enhanced preference for the demonstrated food, occasional observers fail to show an increased preference for the demonstrated food.

It is not clear why certain observers fail to show enhanced preference for socially demonstrated food. Possibly, that is an artifact of the experimental setting in the laboratory, or it may be a result of uncontrolled behavioral variables. Alternatively, there may be a small segment of a social population that is comparatively less successful in exploiting information from their fellows. Individuals who fail to exploit social information about food availability may be poorer foragers than individuals who do use social information. Selective pressure would then favour observers who identified, and avoided, conspecifics that were relatively poor foragers.

Population flux

Poor foragers are more likely to be riskier foragers. Riskier foragers may not be as reproductively successful as their fellows, so selection may have eliminated risky foragers from local populations. However, any given local population may still contain unreliable

demonstrators due to population flux. For example, as a foraging group gets larger, it begins to have more fluctuation in population (Barnett, 1975). Individuals in these larger groups that use social cues for food availability would benefit from the identification of newer and presumably less reliable foragers in a population.

Neophobia

While observers may be selected to discriminate against demonstrators that are unfamiliar with a foraging area, those same demonstrators new to a foraging area may be selected to discriminate against relatively unsuccessful foragers that are established members of a foraging group. For a dietary generalist that is new to a foraging area, there are many possible foodstuffs that could be toxic. One or two demonstrations of safe foods might still leave many unfamiliar foods for the new member of the community to sample. Thus, any interaction with an unfamiliar demonstrator that leads to illness may also result in later discrimination. For the established observer, discrimination would occur because the demonstrator is new and thus unfamiliar with foods in the environment. For the new member of the community, discrimination would occur because the demonstrator was a risky forager.

The new member of the community is possibly in a position similar to the protein-deficient individual. Both need to find nutritionally adequate foods, and both have a potentially large constraint on finding nutritionally adequate food. The new member has the constraint of unfamiliarity with the foraging environment, while the protein-deficient member has the constraint of time to stay alive without adequate nourishment.

In spite of the above possible reasons for discrimination, I failed to find a statistically significant difference in the discrimination tests in these experiments. One reason might be the lack of fluctuation in foraging groups. According to Barnett (1975), Norway rats generally form foraging communities that are remarkably stable. In that case, there would not be as many outsiders; hence, there might not be as many bad foragers. Individuals may also be protected by their neophobia for novel foods. Often, ingestion patterns include a sampling of a novel food, and then further ingestion if the sample does not result in illness. New members of a foraging community might effectively use this technique instead of the potentially time consuming and unreliable method of identifying which conspecifics are good foragers and which are not.

I might not have found an effect due to the robustness of the general transmission of preference. In the basic paradigm, observer rats routinely eat 70-80% of a demonstrated food when offered a choice between that food and another that is equipalatable (see Galef, Attenborough, and Whiskin 1991). Many previous manipulations have not affected this typical result (see Galef, Kennett and Wigmore, 1984).

Another possibility is that there were not enough demonstrations in Experiments 1 through 4. Perhaps two foraging "mistakes" by a demonstrator are not enough to label that demonstrator an unreliable demonstrator. Future studies in this laboratory might investigate discrimination against demonstrators who provide unreliable information more times than the two in the studies presented here.

A gene for a behaviour generally will not spread in a population unless it provides a comparative reproductive advantage over other possible genes at that site. Social

transmission of information is strongest between mothers and offspring (Gerrish and Alberts, 1995). It may be that the adaptation for social extraction of dietary information arose as a general attendance to demonstrators. Because of this adaptation, juveniles learned about edible foodstuffs from their mothers. If Norway rats generally forage in small areas and frequently have prior knowledge of their conspecifics, then a gene that modulates the attendance to particular demonstrators (mothers) at maturity may not provide any advantage to the possible original adaptation that provided a general attendance to demonstrators. If so, Norway rats might not be expected to discriminate against demonstrators. Finally, although social learning exists to provide generalists with information about foods, it may serve other functions as well.

The mechanisms underlying the transmission of food preference remain largely a mystery. The non-significant results in the first part of this thesis prompt further questions attempting to elucidate causal factors in social transmission of preference.

PART II

GENERAL INTRODUCTION

Experiment 1 contained a confound that suggested that familiarity might be an important variable influencing demonstrator quality in the social transmission of food preference. Previous experiments have made observations about the importance of familiarity in the social transmission of food preference. For example, Galef, et. al. (1984) showed that two days of living together did not make a demonstrator "better" for its observer. However, two days might not be enough time to establish a discrimination between familiar and unfamiliar demonstrators.

Empirical data have failed to confirm a situation where a demonstrator voluntarily provides dietary information to a conspecific (e.g. Galef and Dalrymple, 1978). Social transmission appears to be an opportunistic exploitation of information by observers. However, approaching a conspecific to obtain food-related information may carry some risk for an observer. Therefore, observers may be more inclined to acquire social information from relatively familiar conspecifics than from strangers. The investigation of whether familiarity matters in transmission is the focus of the second part of this thesis.

It might also be the case that the association of food ingestion with the conspecific that demonstrated that food made that conspecific more familiar. In other words, in Experiment 1, the unreliable demonstrator is a better demonstrator because it is associated with the food eaten. If so, then general familiarity might be a variable to which observers

attend. In Experiment 5, the influence of demonstrators that had never been out of sensory contact with their observers was compared with that of demonstrators that were completely unfamiliar to their observers.

EXPERIMENT 5

In the present experiment each observer assigned to the familiar condition had lived with its demonstrator all its life, while each observer in the unfamiliar condition never saw its demonstrator prior to interaction on the test day. The independent variable in this experiment was amount of observer familiarity with a particular demonstrator. I hypothesized that an individual that received demonstration from a familiar relative might later show a greater induced preference from that relative than an individual that has demonstration from a completely unfamiliar conspecific.

This experiment had a possible confound between presence of a demonstrator and familiarity of a demonstrator. The observers that had a familiar demonstrator were never out of sensory contact with their demonstrator, which meant that observers in the familiar condition ate with their familiar demonstrator on the other side of a wire grid while those in the unfamiliar condition ate alone. There are two ways that familiarity might affect observer food preference: either through a learned association that conditions preference for a food demonstrated regardless of demonstrator location or by a response that makes attending to demonstration in the presence of a familiar demonstrator more salient than in the presence of an unfamiliar demonstrator. As mentioned above, in the second conceptualization the familiar association would be between the actual demonstrator and the food demonstrated.

Experiment 5 did not show a difference in effectiveness of demonstration between the familiar, present and the unfamiliar, absent demonstrator. Had a significant difference been observed, I would have then proceeded to test whether presence of demonstrator or learned association of familiarity was the variable that caused the difference. It is possible that presence and familiarity have opposite effects on demonstration, which could explain the non-significant findings of Experiment 5.

Method

Subjects

Thirty-six 42-day-old, female Long-Evans rats, born in the McMaster University Vivarium, served as observers, and an additional 36 female Long-Evans rats of the same age as the observers served as demonstrators. The 18 demonstrators and 18 observers in the Unfamiliar Demonstrator (Unfam Dem) group were housed in separate rooms in individual cages measuring 24 cm long x 18 cm high x 18 cm wide, while each of the 18 demonstrators in the Familiar Demonstrator (Fam Dem) group was housed with one of the 18 observers in a 24 x 18 x 18 cm cage. The independent variable was amount of observer exposure to its demonstrator.

Foods

Two foods were composed by mixing powdered Purina Rodent Laboratory Chow #5001 with 1% McCormick's Fancy Ground Cinammon and 1% white sugar (Diet Cin) or 2% Hershey's Pure Cocoa (Diet Coc).

Procedure

Days 1-4 All observers and demonstrators ate Purina Chow from 11:30 AM to 12:30 PM.

Day 5 All demonstrators ate Diet Cin from 10:00 AM to 11:00 AM. Each demonstrator assigned to an observer in the Unfam Dem group ate Diet Cin in a separate room, while each demonstrator assigned to an observer in the Fam Dem group ate Diet Cin on the other side of the partition from its observer. From 11:00 AM to 11:30 AM, each observer interacted with its assigned demonstrator. At 11:30 AM, all demonstrators were returned to their original home cages; all observers were offered a choice between Diet Cin and Diet Coc. Each demonstrator assigned to an observer in the Fam Dem group remained on the other side of the partitioned cage from its familiar observer.

Percent Diet Cin was measured by dividing the total intake of Diet Cin by the total intake of the combination of Diet Cin and Diet Coc. Measurements of intake of Diets Cin and Coc were taken at 1, 3, 6, 24, 48, and 72 hours. Percent Diet Cin was compared for the Unfam Dem and Fam Dem groups at each time interval.

Results and Discussion

After 24 h, a Mann-Whitney U test revealed that observers that had interacted with relatives and eaten in the presence of relatives showed no increase in percent intake of Diet Cin compared to observers that interacted with strangers and ate alone ($U=140$, ns).

In fact, none of the other three time intervals measured during this experiment was even close to significance (1 hour: $U=151.5$, ns; 3 hours: $U=157.5$, ns; 6 hours: $U=145.5$, ns).

Insert Figure 8 About Here

My failure to find a significant result in this experiment suggests that the key criterion for discriminating against conspecifics is not general familiarity. This finding extends Galef et.al.'s (1984) finding that two days of familiarity had no influence on the social transmission of food preference. It might be the case that familiar demonstration is better than unfamiliar demonstration, but feeding in the presence of a demonstrator is worse than feeding alone. This seems unlikely, but perhaps a future experiment will answer that question.

GENERAL DISCUSSION

I found in Experiment 5 that a lifelong familiarity with a related demonstrator is no more likely to induce a preference in an observer than an interaction with an unfamiliar, unrelated conspecific. Clearly, general familiarity is not a factor that observers attend to in the social transmission of food preference. This finding extends an earlier finding from this lab that two days of familiarity did not affect the transmission of preference (Galef, et. al., 1984).

Reciprocal Altruism

Social transmission of food preference might be an example of reciprocal altruism. When an individual performs an act for the benefit of another organism at a cost to the individual performing the act, reciprocal altruism can occur if the individual performing the act has an expectation of a later benefit (Trivers 1971). For example, female vampire bats share blood meals with conspecifics that have foraged unsuccessfully. Later, the meal recipient might forage successfully and share a meal with the original female when she was unsuccessful at foraging (Wilkinson, 1990).

In order for reciprocal altruism to occur, six general parameters must be in place. The individuals involved must have long lives, low dispersal rates, much mutual dependence, little dominance hierarchy, mutual aid in combat, and much parental care (Trivers, 1971). However, reciprocal altruism has been demonstrated in at least one

situation lacking some of the above requirements. Male vampire bats appear to display reciprocal altruism, though male vampire bats don't meet the mutual dependence or low dispersal criteria very well (DeNault and McFarlane, 1995).

In the social transmission of food preference, a demonstrator provides information to an observer about a safe food in their mutual foraging milieu. Resources are often patchily distributed for free-living rats. Therefore, providing information about a safe food may cause a demonstrator to forfeit the opportunity to exploit individually a valuable but scarce food. If the demonstrator expects a future benefit from the observer (in this case, return information about valuable but scarce foods), then it might be worth the cost of losing sole possession of a feeding site. If the demonstrator later receives information from the observer (that is, if the roles are reversed), social transmission of food preference might be a case of reciprocal altruism.

Altruism has had a long and checkered career in the study of animal behaviour. A contender for a general theory of animal behaviour suggested that animals routinely provide conspecifics with free, useful information that can be costly to the provider (Wynne-Edwards, 1962). Wynne-Edwards' theory of group selection, which is predicated upon non-discriminating altruism, has been widely discredited (e.g. Williams, 1966). Furthermore, many effects have been reported that appear to be the result of genuine altruism (e.g. Greene, 1969). More detailed analysis has shown these scenarios are misinterpreted examples of selfish behaviour (e.g. Taylor, 1975).

Therefore, a conclusion that any type of altruism occurs must be made with caution. In the fifth experiment of this thesis, I showed that familiarity was not a strong factor in

the social transmission of preference. Since discrimination based on familiarity and mutual dependence is one of Trivers's important criteria for reciprocal altruism, one might conclude that social transmission is not an example of reciprocal altruism. However, the demonstration periods in Experiment 5 occurred in small cages that probably did not provide the demonstrator an opportunity to hide its information about the safe food it had just eaten. If social transmission were a reciprocally altruistic system, demonstrators should avoid providing information about safe foods to unfamiliar conspecifics. When a demonstrator is stuck in an 18 cm by 18 cm by 24 cm cage with its unfamiliar observer, there may be no way for that demonstrator to avoid transmitting the odour of the food it had recently eaten.

It might also be true that a demonstrator's refusal to allow an unfamiliar conspecific to smell its breath may cause that demonstrator more problems than sharing information would. If a rat is hoarding information from a conspecific about safe foods and is attacked for that behaviour, the damage from being mauled might be much greater than the damage from losing exclusive right to a valuable food site. If so, then the free giving of information, which may look like genuine altruism, is actually the best selfish solution for the forager with the information.

In order to rule out the possibility of reciprocal altruism, an experiment could be run in which a group of rats are living in a large floor cage. If demonstrators are just as willing to be approached by strangers as familiar cage mates before and after eating novel foods, we might conclude that there is no discrimination based on familiarity and hence probably no reciprocal altruism. If, however, demonstrators are equally willing to be

approached by familiar cage mates before and after eating but avoid strangers much more after eating than before, we might conclude that there is discrimination against strangers in food information sharing. A reciprocally altruistic system would still be a possibility.

Pseudo-reciprocity

A model that probably more accurately describes food information sharing is pseudo-reciprocity, or mutualism. In a case of pseudo-reciprocity, the return benefit for a beneficent act is a result of selfish behaviour on the part of the recipient of the original act (Connor, 1986). For example, in reciprocal altruism, the first individual (A) incurs some personal cost for the benefit of another individual (B). The system is stable because there is a high probability that B will later incur a cost for the sake of the benefit of A. In pseudo-reciprocity, A incurs some cost for the benefit of B, and A then gains a later benefit as a by-product of a selfish act on the part of B. In reciprocal altruism, B returns the favour by incurring a later cost for the benefit of A; in pseudo-reciprocity B later acts selfishly (at little personal cost) but provides a residual benefit to A.

Social transmission of food preference might be a form of pseudo-reciprocity if the observer in a social transmission situation remains in a foraging group for the selfish purpose of continually receiving information about safe foods to eat. In doing so, the observer (B in the model above) will frequently have received information about a safe food from a third conspecific (C). If B then passes along the information to A, A gains a residual benefit from B remaining in the community. The observer (B) happens to return a

favour to the original demonstrator (A), but the observer is also selfishly increasing its own ability to reproduce.

However, mutualism may be less likely to occur if familiar conspecifics are not better demonstrators than unfamiliar conspecifics. Potentially B is sharing information with A about the safe food B ate because such sharing is a prerequisite for membership in the foraging community. If so, B might be selected to avoid providing information to strangers, since a stranger is not a member of the foraging community of A and B.

Individual Discrimination

There is evidence that many species of rodent are able to discriminate conspecifics based on odour cues. Meadow voles (Ferkin, 1988), Colombian ground squirrels (Hare, 1994), kangaroo rats (Randall, 1991), mice (Kareem, 1983; Corridi, et. al., 1993) and Belding's ground squirrels (Holmes, 1986) have some type of specialized discrimination of individuals based on odour cues. The Norway rat is able to make associative discrimination for food rewards when the conditioned stimulus is a familiar or an unfamiliar rat (Krames, 1970). Thus, the results of Experiment 5 probably can not be interpreted as an artifact of a demonstrator's inability to recognize an individual.

Many of the rodent species mentioned above have more agonistic interactions with familiar conspecifics than strangers. For example, Ferkin's (1988) study found that male meadow voles had a higher proportion of hostile encounters with familiar conspecifics than with unfamiliar conspecifics. This result is attributed to male meadow voles'

polygamy; hostility toward one's neighbour may increase one's chances of stealing copulation with a neighbour's mate.

Corridi et. al. (1993) found that familiarity with a conspecific's odour, without interaction with that conspecific, led to increased hostility in the mouse when interaction occurred. However, Kareem (1983) discovered that familiarity with a conspecific leads to decreased hostile interactions. These results suggest that in the mouse, when an individual has experience with another individual, there is decreased hostility due to the establishment of a hierarchy. Unfamiliarity with a conspecific implies no dominance hierarchy; thus hostility arises in the competitive creation of a hierarchy.

The fact that familiarity leads to a decrease in agonistic interaction might have suggested that Experiment 5 would have showed an advantage for the "familiar demonstrator" group, since that group had an established dominance hierarchy. However, Experiment 5 used females, which are generally less likely to establish rigid dominance hierarchies. A future experiment may replicate Experiment 5 with males and establish whether scuffles over the creation of a dominance hierarchy inhibit social transmission for unfamiliar demonstrator-observer pairs.

General Dietary Safety

Finally, there must be some correlation between attending to familiar demonstrators and improved dietary safety in order for such discrimination to be selectively advantageous. If the demonstration of a food almost inevitably implies that the demonstrator ate a safe food, then an observer would not benefit by only attending to the

messages of familiar conspecifics. It is possible that nomadic individuals temporarily enter a rat community, but in many rat communities this is not the norm (Barnett, 1975).

Therefore, if all demonstrators that a particular observer encounters are equally qualified to provide good demonstration, that observer would not benefit by discriminatively attending to familiar demonstrators. The observer would lose the advantage of all the information provided by comparatively unfamiliar observers, and thus that observer would be at a competitive disadvantage compared to conspecifics that did not discriminate between familiar and unfamiliar demonstrators.

Future experiments may investigate the role of familiarity in social transmission for rats that live in larger communities. These larger communities generally have greater flux, and possibly more members that are temporary and thus dangerous foragers. An observer might be selected to discriminate against such unreliable nomads. Whatever the answer to that question, there is still much to be discovered about the role of familiarity in the social transmission of food preference.

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FIGURE CAPTIONS

- Figure 1. Mean cumulative amount of Diet Cin eaten in Experiment 1 as a percentage of total intake, by observers whose demonstrators had either previously demonstrated an illness-inducing diet or were unfamiliar.
- Figure 2. Mean amount of Diet Cin eaten in Experiment 1 as a percentage of total intake and measured over non-cumulative time intervals, by observers whose demonstrators had previously demonstrated either an illness-inducing diet or an irrelevant diet.
- Figure 3. Mean amount of Diet Cin eaten in Experiment 2 as a percentage of total intake, by observers whose demonstrators ate either Diet Cin or Diet Coc and had previously demonstrated either an illness-inducing diet or an irrelevant diet.
- Figure 4. Mean cumulative amount of Diet Cin eaten in Experiment 3 as a percentage of total intake, by observers whose demonstrators had either previously demonstrated an illness-inducing diet or previously demonstrated a diet that was safely ingested by the observers.
- Figure 5. Mean amount of Diet Cin eaten in Experiment 3 as a percentage of total intake and measured over non-cumulative time intervals, by observers whose demonstrators had previously demonstrated an illness-inducing diet or had previously demonstrated a diet later safely ingested.
- Figure 6. Mean amount of Diet Cin eaten in Experiment 4 as a percentage of total intake, by protein-deplete observers whose demonstrators had either previously demonstrated a protein-deplete diet or were unfamiliar.
- Figure 7. Mean amount of Diet Cin eaten in Experiment 5 as a percentage of total intake, by observers whose demonstrators had either never been out of sensory contact with their observers or were unfamiliar to their observers.
- Figure 8. Mean amount of Diet Cin eaten in Experiment 5 as a percentage of total intake and measured over non-cumulative time intervals, by observers whose demonstrators had either never been out of sensory contact with their observers or were unfamiliar to their observers.

FIGURE 1

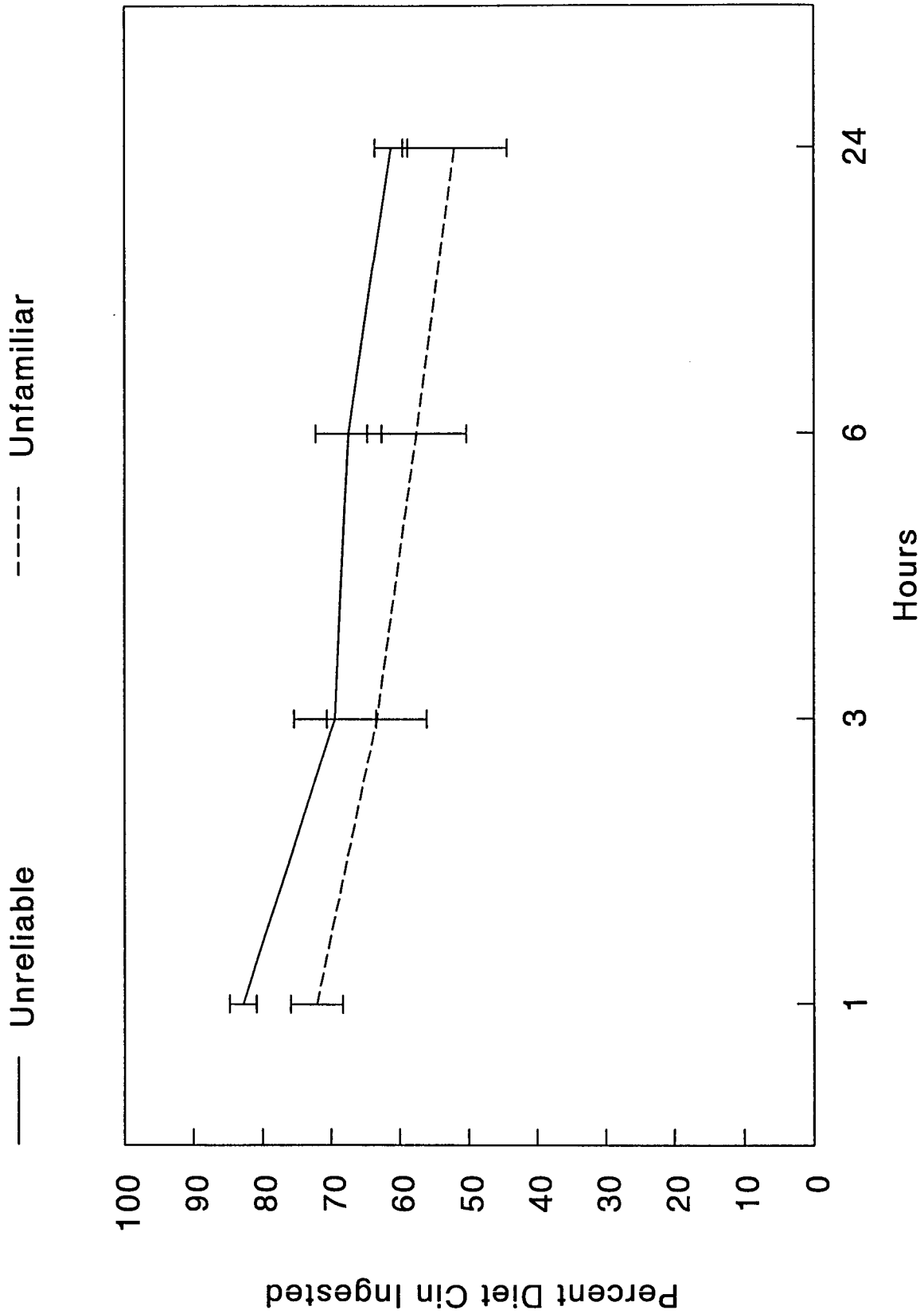


FIGURE 2

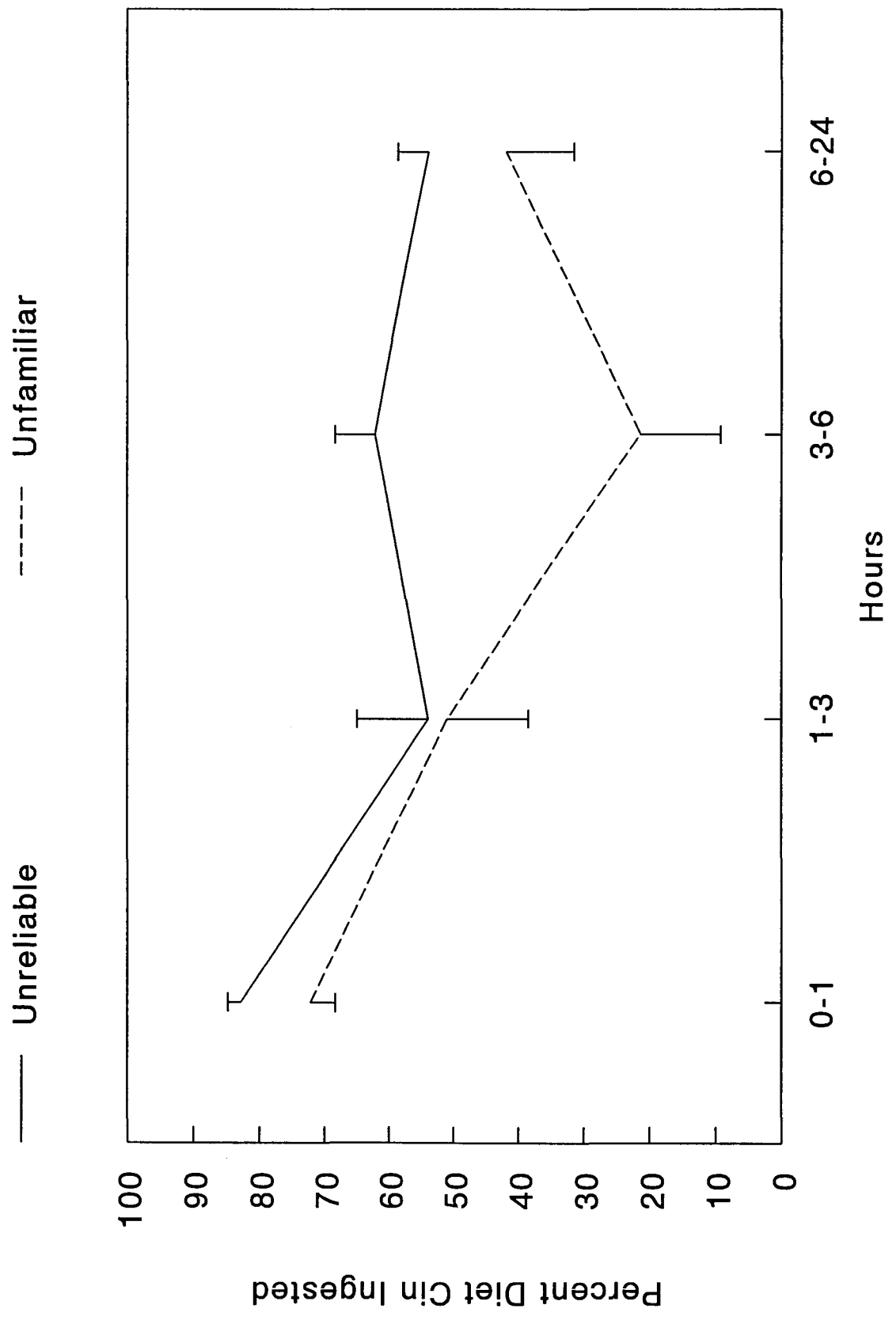


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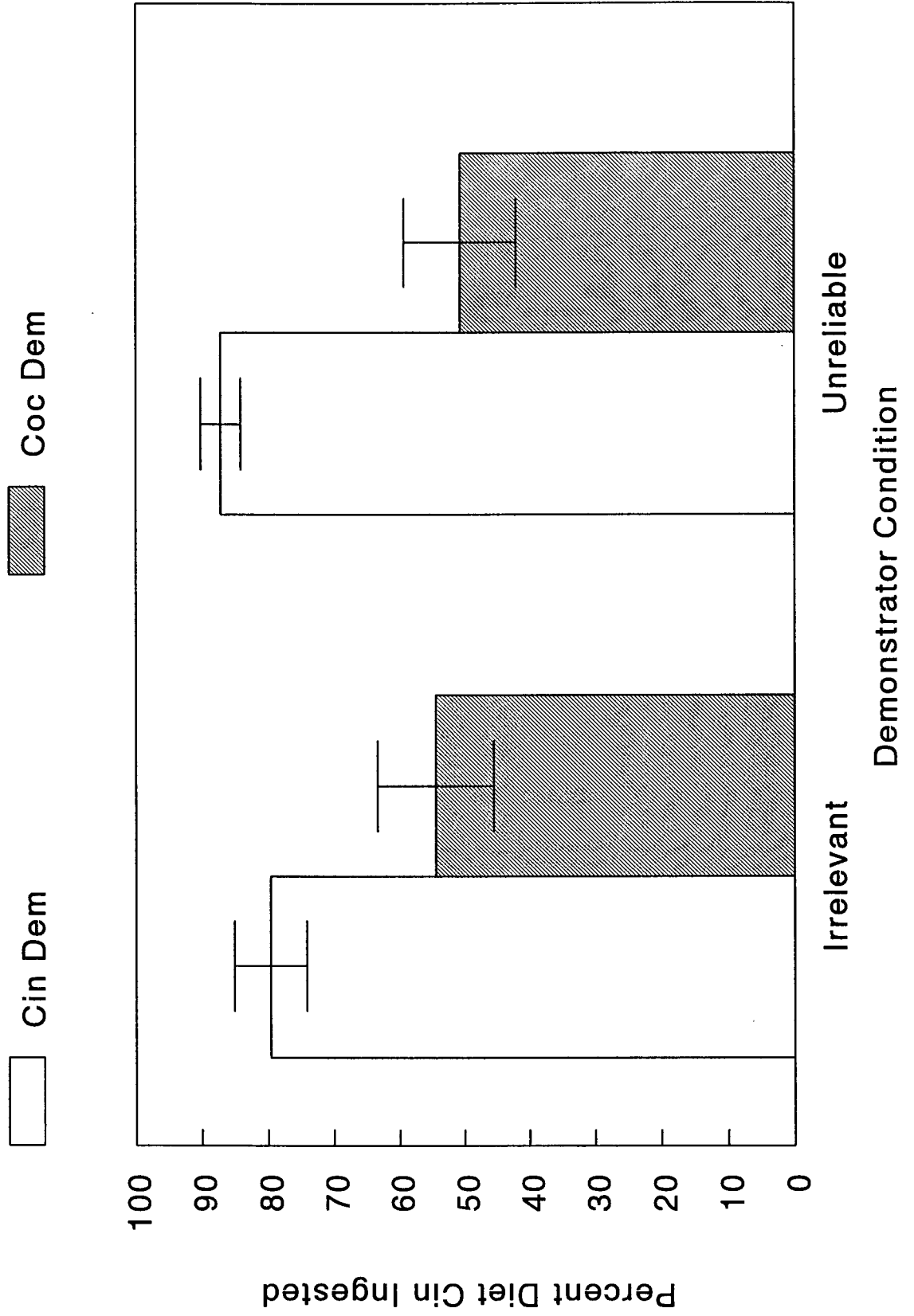


FIGURE 4

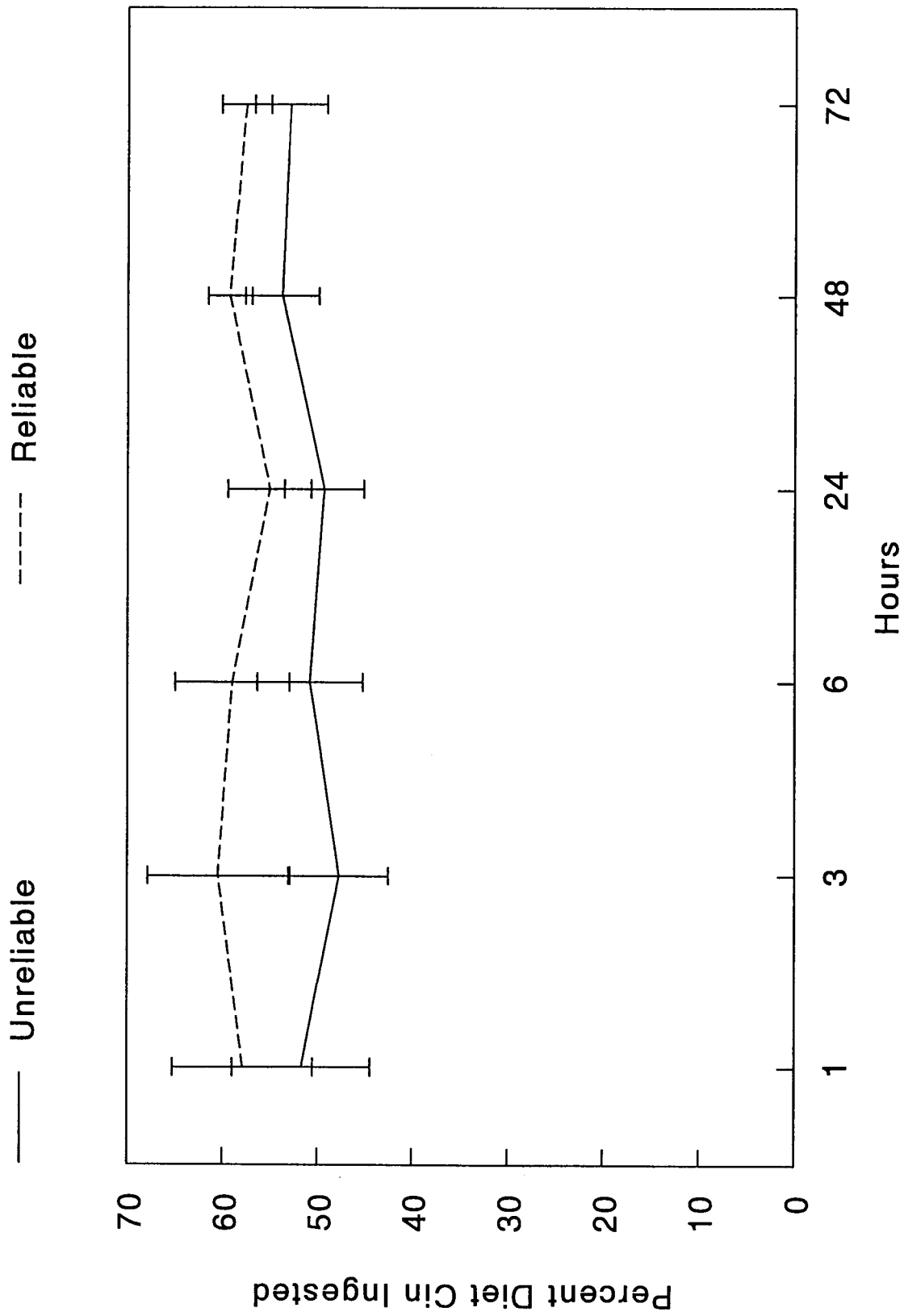
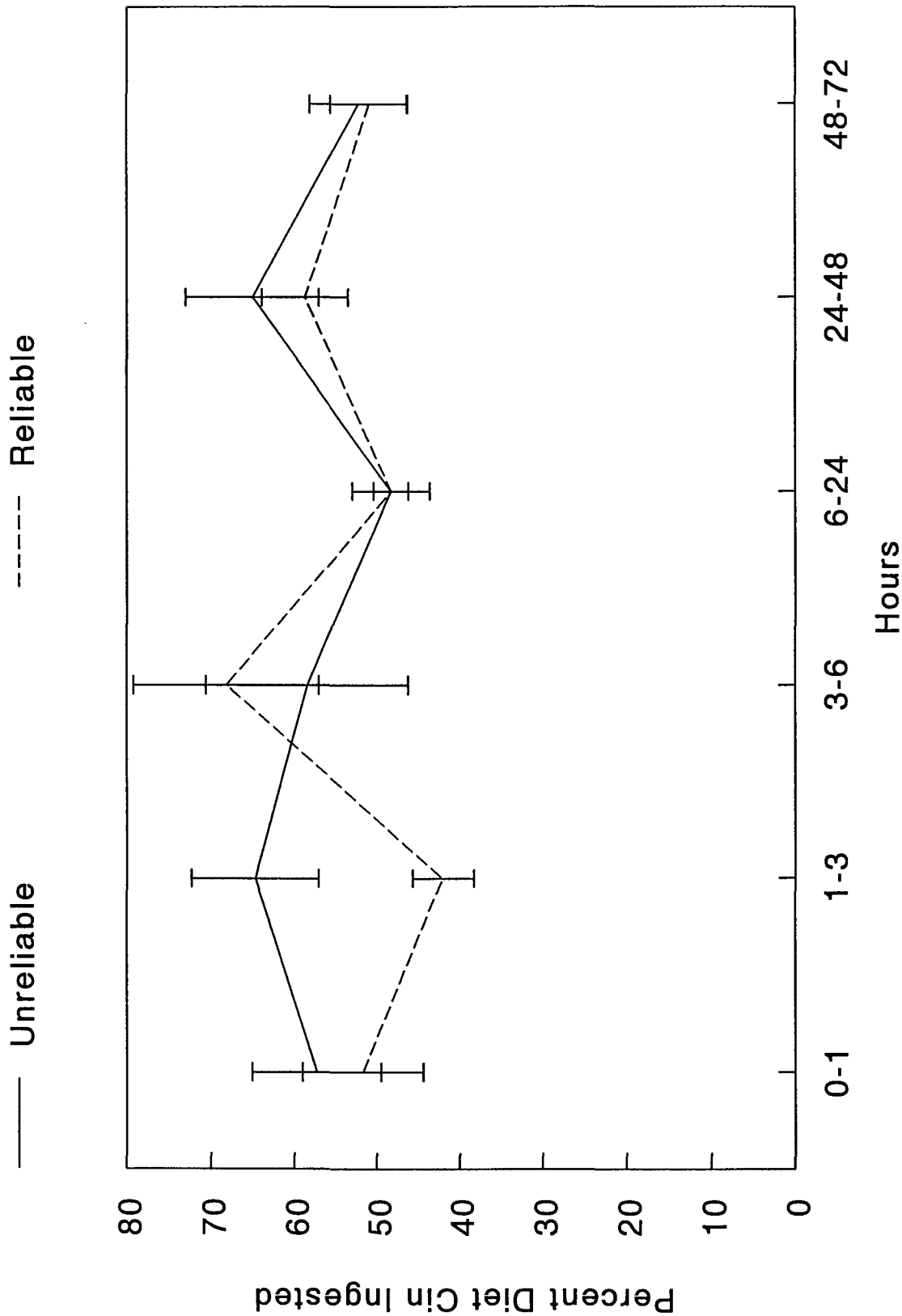


FIGURE 5



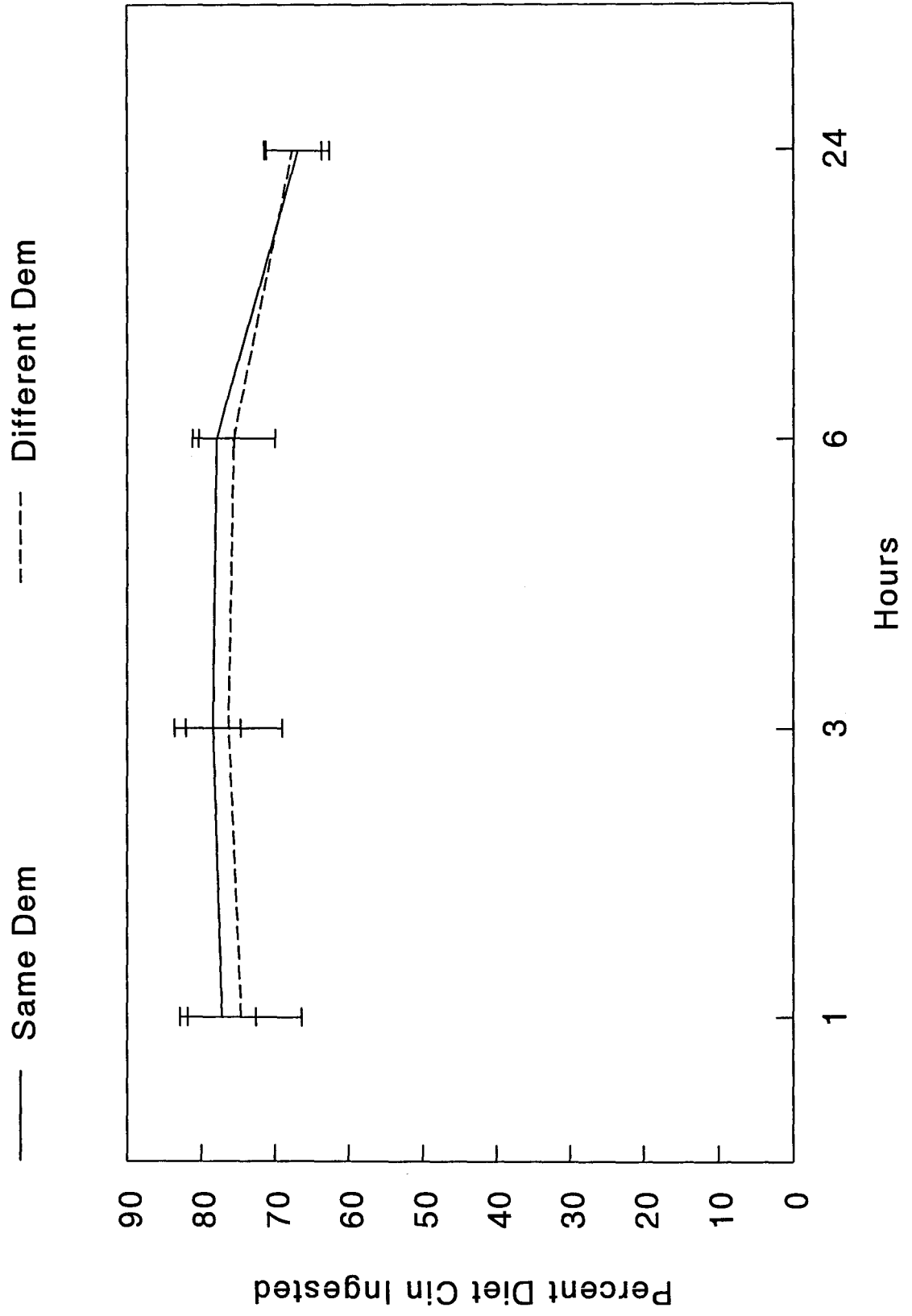


FIGURE 7

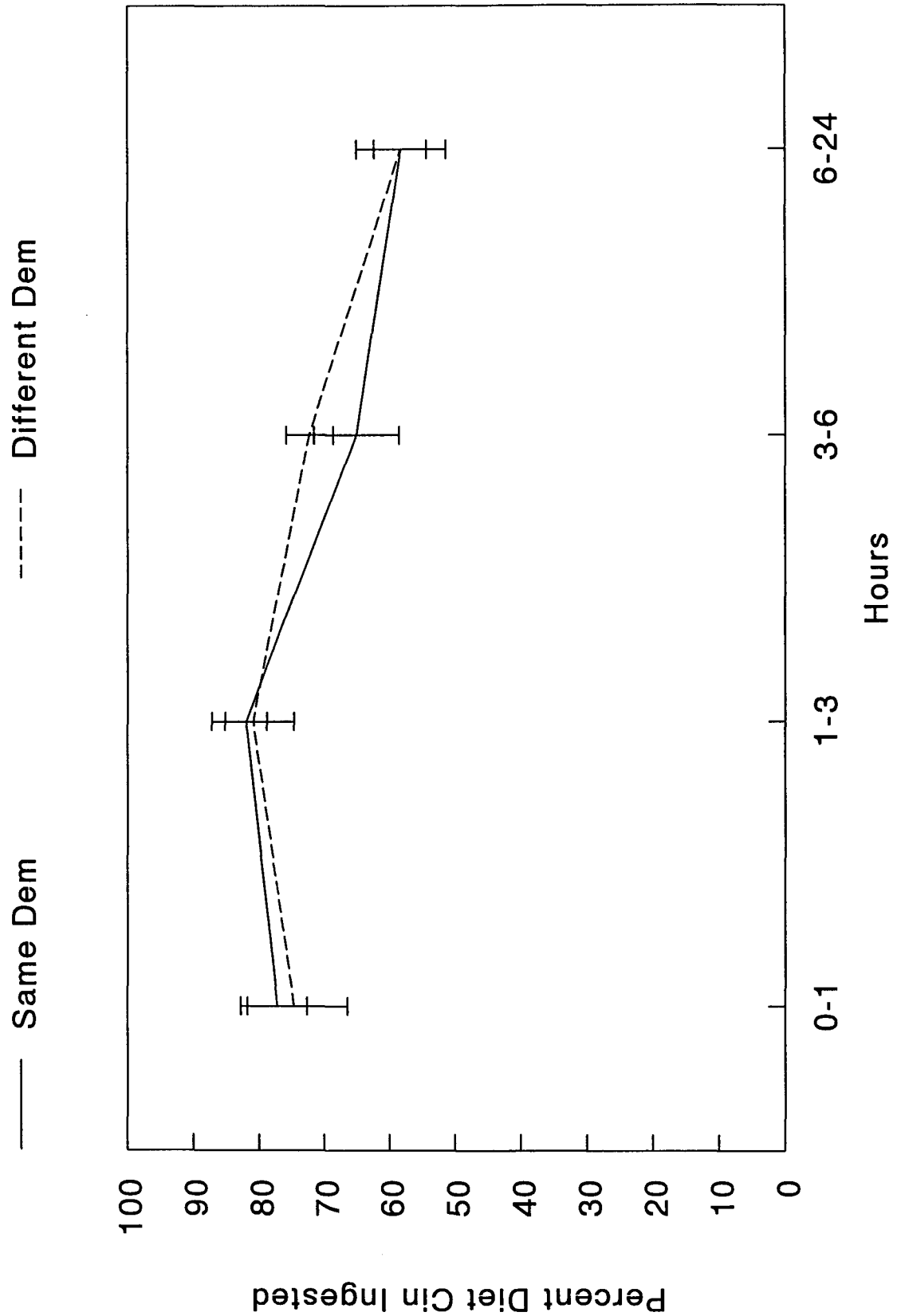


FIGURE 8

