

INTERACTIONS BETWEEN SOCIAL LEARNING
STRATEGIES

INTERACTIONS BETWEEN COPY-WHEN AND COPY-WHO STRATEGIES OF
SOCIAL LEARNING

By

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A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Master of Science

McMaster University

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MASTER OF SCIENCE (2008)

McMaster University

(Psychology, Neuroscience and Behaviour)

Hamilton, Ontario

TITLE: Interactions between copy-when and copy-who strategies of social learning

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NUMBER OF PAGES: vii, 39

ABSTRACT

Theoretical models predict conditions under which individuals should forgo individual learning and instead copy the behaviours of others. These predictions are categorized as copy-when and copy-who social learning strategies, and pertain to *when* an individual should rely on social learning to guide its behaviour and *whom* that individual should select as a demonstrator. In general, and particularly in Norway rats (*Rattus norvegicus*), there is greater empirical support for copy-when than copy-who strategies. In this thesis, we present a novel approach to the study of social learning in hypothesizing that interactions exist between copy-when and copy-who strategies that predispose individuals to be more discriminating when choosing whom to copy. Consequently, the failure of some studies to find evidence of copy-who strategies may be due, in part, to experimental protocols that did not incorporate critical copy-when variables. We tested the prediction that ‘observer’ Norway rats would preferentially copy successful over unsuccessful demonstrators when uncertain about the relative safety of two novel foods, but not when certain. The results of two experiments presented herein, confirm our prediction that observer rats do copy successful demonstrators when uncertain. Additionally these results are the first to show that Norway rats actively select particular conspecifics to serve as models when choosing whom to copy. Further investigation of similar interactions between copy-when and copy-who strategies promises to be a rewarding avenue of research for both theoretical and empirical studies of social learning.

ACKNOWLEDGMENTS

I am much appreciative of Dr. Jeff Galef for being an excellent mentor, supervisor and collaborator over the course of this year. I also greatly appreciate the helpful discussions and comments on my work provided by Dr. Margo Wilson and Dr. Sigal Balshine. These experiments could not have been done without the superb assistance of Elaine Whiskin: the original rat-whisperer and first-class teacher of all things *Rattus norvegicus* and otherwise. Many thanks also to Dr. Galef and Mrs. Lesley Taylor for their helpful comments on my thesis, and to Reuven Dukas for his support and comments on the final draft. This work was funded by the Natural Sciences and Engineering Research Council of Canada.

TABLE OF CONTENTS

MANUSCRIPT

Introduction.....	1
Experiment 1: Copy successful individuals when uncertain.....	5
<i>Method</i>	6
<i>Results and Discussion</i>	9
Experiment 2: Certain observers.....	11
<i>Method</i>	12
<i>Results and Discussion</i>	13
General Discussion.....	14

APPENDIX

Introduction.....	18
General Methods.....	18
Experiment 3: Copy successful individuals when individual learning is costly.....	22
<i>Method</i>	23
<i>Results and Discussion</i>	24
Experiment 4: Copy successful individuals when uncertain.....	27
<i>Method</i>	27
<i>Results and Discussion</i>	28
Conclusions.....	30
Figure Captions	32
Figures	33
References	37

FIGURES

Figure 1: Mean (± 1 SEM) percent of demonstrator's diet eaten by uncertain observers that had interacted with either ill or healthy demonstrators in experiment 1. Numbers inside histograms = N per group

Figure 2: Mean (± 1 SEM) percent of demonstrator's diet eaten by certain observers that had interacted with either ill or healthy demonstrators in experiment 2. Numbers inside histograms = N per group

Figure 3: Mean (± 1 SEM) percent of healthy demonstrator's diet eaten by observers whose prior personal learning experience was either costly (LiCl Obs) or not (Sal Obs). Numbers inside histograms = N per group

Figure 4: Mean (± 1 SEM) percent of healthy demonstrators' diets eaten by certain and uncertain observers. Numbers inside histograms = N per group

Early discussions of social learning presumed that copying the behaviours of others was an inherently adaptive strategy, but this notion was rejected in the 1980s by theoretical models and the ensuing empirical work they inspired (Barnard & Sibley, 1981; Boyd & Richerson, 1985). Theoreticians have since proposed a number of models, summarized in Laland (2004), that predict both *when* an individual should rely on socially acquired information to guide its behaviour (copy-when strategies), and *from whom* information should be gleaned (copy-who strategies). Presently, there is far greater empirical support for predictions concerning copy-when than copy-who strategies. In Norway rats (*Rattus norvegicus*), for example, although seven copy-who strategies have been tested, only copy-the-majority has received empirical support, whereas other studies provide support for three of four copy-when strategies examined to date: copy when uncertain, dissatisfied, and when individual learning is unproductive (Chou & Richerson, 1992; Galef & Whiskin, 2008; Galef, Dudley, & Whiskin, 2008).

Here, we present the first empirical support for the copy-who strategy *copy-successful-individuals*. We investigated an interaction between two social learning strategies, one that is well established in the literature (copy-when-uncertain), and a second for which there is, as yet, no empirical support (copy-successful-individuals).

Copy-when-uncertain

Copy-when-uncertain is a “when” strategy that has received considerable empirical support (Laland, 2004). For example, Kendal et al. (2004) found that during a choice test, guppies (*Poecilia reticulata*) that were naïve (and thus uncertain) regarding

the presence or absence of food at each of two feeders, swam to the feeder where they had observed conspecifics forage but not to the second, unvisited feeder. However, guppies that had reliable personal information regarding the presence of food at the feeders, and were therefore ‘certain’, ignored social information and instead chose where to forage based on their personal experience (Kendal, Coolen, & Laland, 2004).

More relevant to the present experiments, Galef and colleagues demonstrated that Norway rats presented with two novel foods reliably prefer the diet eaten by conspecifics, as communicated by odor cues on their breath (Galef, 1996). The magnitude of such social learning is reduced, however, when observer rats have previously eaten the diets eaten by their demonstrators and are therefore “certain” from personal experience about the safety and value of those diets (Galef & Whiskin, 1994). Galef et al. (2008) also made Norway rats certain or uncertain regarding the causal relationship between eating an unfamiliar food and gastrointestinal upset. Before receiving an illness-inducing injection, “certain” observer rats ate a cinnamon-flavoured diet whereas “uncertain” rats ate a dual-flavoured diet (cinnamon-and-cocoa). The certain observers could therefore be confident that eating cinnamon caused their illness, whereas the uncertain observers could not know whether cinnamon, cocoa or their combination was responsible. Certain and uncertain observers subsequently interacted with a demonstrator rat that had recently eaten either anise- or marjoram-flavoured food. Later, during a food preference test between anise- and marjoram-flavoured diets, uncertain observers ate significantly more of their demonstrators’ diets than certain observers, as copy-when-uncertain would predict (Galef et al., 2008).

Copy-successful-individuals

Because members of a population inevitably vary in traits such as age, health, kinship, and social rank, the social information an individual provides will vary in both its quality and its relevance to an observer. Consequently, theory predicts that characteristics of a demonstrator and prospective observer interact to affect the probability of social learning (Coussi-Korbel & Frigaszy, 1995).

Few studies in rats have found evidence of such discriminate social learning, defined as the preferential adoption of behaviours of conspecifics based on their characteristics. For example, experiments have, thus far, failed to provide evidence that Norway rats choosing between diets rely more heavily, as theory predicts they would, on reliable than unreliable demonstrators, kin than non-kin, or successful than unsuccessful demonstrators (Galef, 1996; Galef & Whiskin, In press).

The *copy-successful-individuals* strategy is of particular interest because an observer clearly stands to gain more from copying the behaviour of successful, than of unsuccessful, demonstrators (Laland, 2004). However, despite the reduced expected benefit associated with copying unsuccessful demonstrators, several studies have found that animals are indiscriminate regarding from whom they learn. For example, domestic hens (*Gallus gallus*) do not discriminate between successful and unsuccessful demonstrators when learning to perform an operant discrimination task for food (Nicol & Pope, 1999). Similarly, although rats are quite capable of distinguishing between poisoned and unpoisoned demonstrators, observer rats will adopt the food choices of ill and healthy demonstrators with equal probability (Galef, Wigmore, & Kennett, 1983;

Galef, McQuoid, & Whiskin, 1990). There is evidence, however, in some species, of attention to the success of potential demonstrators. For example, bats (*Nycticeius humeralis*) that have been previously unsuccessful at foraging will follow successful individuals from a roost to feeding sites (Wilkinson, 1992) and, redwing blackbirds (*Agelaius phoeniceus*) are more likely to adopt the food preference of a conspecific when that individual remains well after eating than if it becomes ill (Mason, 1988).

Two, non-mutually exclusive, explanations may account for such inconsistent empirical findings regarding the theoretical prediction *copy-successful-individuals*. First, the natural history of a species may determine whether a particular social learning strategy is indeed adaptive, and second, some strategies may be employed within a narrow range of environmental parameters, thus making evidence of them difficult to discover.

Present Research

The failure of empirical studies to support theoretical models suggests either that theory is incorrect, at least for some animal models, or more probably that the experimental protocols used to test predictions from theory are somehow inadequate. Given the complexity of both the social and physical environment of animals in nature, the rules that govern when *copy when* and *copy who* strategies are used are likely to be sensitive to environmental parameters, internal states and their interactions. We hypothesized that an interaction may exist between *copy when* and *copy who* strategies

and consequently, experiments that evaluate *copy who* strategies by altering only one parameter in isolation may not elicit discriminate social learning.

We tested this hypothesis in Norway rats in two experiments that integrated *copy-successful-individuals* and *copy-when-uncertain* social learning strategies. If observer rats copy successful individuals when they are uncertain, then we will have 1) demonstrated that Norway rats are capable of discriminate social learning, 2) provided the first empirical support, in rats, for the *copy-successful-individuals* strategy and 3) introduced a novel approach to examining the dynamics of social learning strategies.

EXPERIMENT 1 – Copy successful individuals when uncertain

Despite considerable effort, results of many studies from our laboratory have failed to provide evidence of either social transmission of food aversions or discriminate social learning in Norway rats (Galef et al., 1983; Galef et al., 1990; Galef & Whiskin, 2000). However, a paper by Hishimura (2000) may provide evidence of both phenomena. Hishimura (2000) fed observer rats two novel diets sequentially and poisoned the rats 1 hr after they ate. These rats later interacted with either a poisoned or an unpoisoned conspecific demonstrator that had recently eaten one of the two diets fed to the observers. Results of a subsequent food preference test suggested that rats that interacted with a poisoned demonstrator avoided the diet it ate, whereas rats that interacted with an unpoisoned demonstrator did not show a similar socially mediated food aversion. Hishimura's (2000) experiment is the first that has not failed in replication to demonstrate

both socially transmitted food aversions and discriminate social learning in rats, and accordingly, warranted further examination.

In experiment 1, we sought to repeat the findings of Hishimura (2000) because, although not his intent, Hishimura's protocol may have resulted in a scenario that elicits use of both "copy when" and "copy who" strategies. Examination of Hishimura's paper raised methodological concerns and we therefore altered his protocol to address them accordingly. Our goal was to make observer rats uncertain as to which of two diets caused brief gastrointestinal upset and then to present them with either successful or unsuccessful demonstrators. We predicted that uncertainty would increase the value of socially acquired information and, might therefore, increase the probability that observers would attend to the qualities of their demonstrators when deciding whether to rely on the information that they provided. In light of previous experimental results from our laboratory, we did not expect to find the socially transmitted flavour aversions Hishimura (2000) reported, and instead predicted that all observers, regardless of prior treatment, would show a preference for the diets eaten by their respective demonstrator (Galef et al., 1990). However, we expected that uncertain observers would be more likely to use information acquired from successful than unsuccessful demonstrators.

Method

Subjects

Ninety-nine experimentally naïve, female Norway rats, acquired from Charles River Canada (St. Constant, Quebec), served as observers when 8- to 9-weeks old. We

randomly assigned observers to one of two groups: approximately half of the observers interacted with a healthy, and therefore successful, saline-injected demonstrator ($N = 49$) and the remaining observers interacted with an ill, and therefore unsuccessful, lithium chloride-injected demonstrator ($N = 50$).

Eighty-one additional female Norway rats that had served as observers in prior experiments on social transmission of food preferences served here, when 9- to 16-weeks old, as demonstrators. Eighteen of these rats served twice as demonstrators during the experiment. The experiment was carried out in three replicates over the course of 6 weeks.

Apparatus

For the duration of the experiment, we housed subjects individually in stainless-steel hanging cages, measuring 35 x 18 x 21 cm, where they had ad libitum access to water. Subjects ate from semi-circular, stainless-steel food cups, measuring 10 cm in diameter and 5 cm in depth, attached to one side of each cage.

Diets

We prepared two diets by mixing powdered diet 8640 (Harlan-Teklad, Madison, Wisconsin, U.S.A.) with either 1.5% by weight ground anise (diet ani: The Horn of Plenty, Dundas, Ontario, Canada) or 1% by weight ground cinnamon (diet cin: McCormick's Canada, London, Ontario).

Procedure

Step 1: Food Deprivation

To ensure that rats would eat promptly when presented with food during the experiment, we fed both observers and demonstrators powdered diet 8640 at the same hour for 1 hr/day, for 3 consecutive days.

Step 2: Observer pre-conditioning

On the 4th day of scheduled feeding, for 15 min, we gave 49 observer rats a weighed food cup containing diet ani and the remainder a food cup containing diet cin. After 15 min, we removed this food cup and, for 15 min, gave each observer a second weighed food cup, containing the other diet. At the end of each 15-min feeding period, we weighed food cups to ensure that each observer ate a minimum of 1.0 g of each diet.

One hour after removing the second food cup, we injected each observer intraperitoneally with 0.13 M LiCl solution, equivalent in volume to 2% of its body weight. For approximately 15 min following the LiCl injection, observers experienced a bout of mild gastrointestinal upset, including diarrhea. One hour after injection, we provided each observer with ad lib access to powdered diet 8640 for 23 hr.

Step 3: Interaction with demonstrators

We randomly assigned observers to interact with either healthy (successful) demonstrators or ill (unsuccessful) demonstrators, as determined by the nature of the injection the demonstrators received.

For 1 hr on day 5, before demonstrators interacted with observers, we gave half of the demonstrators assigned to each condition (healthy and ill) a weighed food cup containing diet ani and the remaining demonstrators, a weighed food cup containing diet cin. After this 1-hr feeding, we removed food cups and weighed them to ensure that each demonstrator had eaten a minimum of 3.0 g. We then injected demonstrators assigned to the healthy condition intraperitoneally with isotonic saline, and those assigned to the ill condition with 0.13 M LiCl solution, equivalent in volume to 2% body weight. Next, we placed each demonstrator into the cage of an observer and allowed demonstrators and observers to interact for 30 min.

Step 4: Food preference test

Immediately following step 3, we removed demonstrators from observers' cages and gave each observer two weighed food cups, one containing diet ani and the other diet cin. We weighed the food cups 10 and 23 hr later and determined the proportion of demonstrator's diet eaten by each observer.

Results and Discussion

We removed ten observers from the experiment: eight because they failed to eat a minimum of 1 g of either diet ani or cin during the initial 15-min feedings (step 2); one because its demonstrator did not eat 3.0 g during step 3 and one because it spilled its food during the food-preference test (step 4).

The main results of experiment 1 are presented in Figure 1 which shows the mean amount of healthy and ill demonstrators' diets eaten by each observer, as a percentage of the total amount of food it consumed during both the first 10 hr and 10th to 23rd hr of the food-preference test (step 4). Observers that interacted with healthy demonstrators ate more of their respective demonstrators' diets during testing than observers that interacted with ill demonstrators (Repeated Measures ANOVA, with arcsine square root transformation: $F_{1, 65} = 6.40, P < 0.014$).

Although the observers in each replicate tended to prefer the diets eaten by their healthy demonstrators, this tendency was not always significant (Replicate 1: $F_{1, 27} = 4.54, P < 0.04$; Replicate 2: $F_{1, 20} = 0.42, P = 0.53$; Replicate 3: $F_{1, 26} = 3.51, P = 0.07$). However, we found no difference between replicates ($F_{2, 65} = 1.47, P = 0.24$), suggesting that our protocol elicited weak, but reliable discriminate social learning by observer rats.

During the 23-hr food preference test, demonstrators' state (healthy/ill) had no effect on the total amount of food eaten by observers (mean \pm SEM eaten by observers with ill demonstrators: 20.9 ± 0.6 g; observers with healthy demonstrators: 21.6 ± 0.6 g; Student's t test: $t_{86} = -0.84, P = 0.40$)

As found in previous experiments conducted in our laboratory (Galef et al., 1983; Galef et al., 1990), during the 23-hr test, all observers preferred the diet eaten by their respective demonstrator, regardless of whether their demonstrator was healthy or ill (one-sample t test: $70.4 \pm 3.6\%$; $t_{87} = 5.73, P < 0.001$; Fig. 1). Thus, although observers discriminated between successful and unsuccessful demonstrators when uncertain as to the relative safety of two foods, they did not acquire socially transmitted food aversions

after interacting with ill demonstrators. The finding in the present experiment, that all observers preferred their demonstrators' diets, differs from Hishimura's (2000) finding that observer rats that interacted with poisoned demonstrators ate only approximately 35 percent of their respective demonstrators' diets. However, the observers in Hishimura's study that interacted with non-poisoned demonstrators showed only a moderate preference for that demonstrator's diet (approximate mean of 55%), a finding that is highly inconsistent with decades of work reporting robust socially enhanced food preferences in rats (Galef & Wigmore, 1983; Galef et al., 1983; Heyes & Durlach, 1990).

EXPERIMENT 2 – Certain Observers

The previous experiment was conducted to repeat Hishimura's (2000) finding of discriminate social learning in rats. However, the protocol did not allow us to determine whether, as description of observers as 'uncertain' requires, observers' had to learn an association between illness and the two diets that they ate during step 2.

Experiment 2 was conducted to determine whether it was necessary for observers to first learn that one or both foods were associated with subsequent illness in order for them to later discriminate between quality of demonstrators. Possibly, in experiment 1, experience of illness or simple exposure to the two diets used in steps 2 and 4 was sufficient to cause observers to become more discriminating when adopting socially acquired food preferences. If so, our prediction, that observer rats will copy successful individuals when uncertain, would not be supported by the results of experiment 1.

In experiment 2, all observers experienced both the two novel foods and injection with a toxin. However, we reversed the order of these events so that observers would not associate the flavour of the foods with illness. We predicted that, in the absence of experience necessary to produce uncertainty as to the safety of cin- and ani-flavoured diets, observers with ill and healthy demonstrators would not differ in the proportion of their demonstrators' diets that they ate during the food-preference test.

Method

Subjects

Sixty, experimentally naïve, female Norway rats, acquired from Charles River Canada (St. Constant, Quebec), served as observers when 8- to 9-weeks old. We randomly assigned half of the observers to interact with a healthy (saline-injected) demonstrator ($N = 30$) and half to interact with an ill (lithium chloride-injected) demonstrator ($N = 30$).

Sixty additional female Norway rats that had served as observers in previous experiments on social transmission of food preferences served as demonstrators when 9- to 16-weeks of age.

Procedure

The methods for this experiment were identical to those of experiment 1, with the exception that we reversed the order of events in Step 2; we injected observers with LiCl 2 hr before we exposed them to diets ani and cin, each for 15 min. We carried out this experiment in two replicates.

Results and Discussion

We removed five observers from the experiment because they failed to eat a minimum of 1 g of either diet ani or cin during step 2.

The main results of experiment 2 are presented in Figure 2, which shows the mean percentage of demonstrators' diets eaten by observers during the food-preference test (step 4). Unlike observers in experiment 1, observers in experiment 2 did not eat a greater percentage of the diet that their respective demonstrator had eaten when their demonstrator was healthy compared to when it was ill. (Repeated Measures ANOVA, with arcsine square root transformation: $F_{1, 39} = 0.01$, $P = 0.97$).

During the 23-hr food preference test (step 4), the total amount of food observers ate was unaffected by the state of health of their respective demonstrators (mean \pm SEM amount eaten by observers with ill demonstrators: 20.4 ± 0.6 g and by observers with healthy demonstrators: 20.5 ± 0.5 g; Student's t test: $t_{53} = -0.09$, $P = 0.92$)

As in experiment 1, we found no difference between replicates ($F_{1, 39} = 1.19$, $P = 0.28$), and no evidence of socially transmitted flavour aversions; observers that interacted with ill demonstrators (one-sample t test: $t_{26} = 2.74$, $P < 0.01$), like those that interacted

with healthy demonstrators ($t_{27} = 3.77, P < 0.001$), preferred their demonstrator's diet during the 23-hr food preference test (Fig. 2).

When observers in experiment 2 experienced both two novel foods and gastrointestinal upset and these events were not presented in a fashion that would lead the observers to learn an aversion to the foods and, presumably, become uncertain as to which food made them ill, the observers did not show discriminate social learning. Like observers in previous experiments conducted in our laboratory (Galef et al., 1983; Galef et al., 1990) in which uncertainty was not induced in observers before they interacted with demonstrators, observers in the present experiment were as likely to adopt the food choices of ill as of healthy demonstrators.

GENERAL DISCUSSION

The greater preference of observers, in experiment 1, for the diets of healthy than of ill demonstrators is consistent with theoretical predictions that individuals should preferentially adopt the behaviours of successful conspecifics (Boyd & Richerson, 1988; Laland, 2004). To our knowledge, this is the first replicated report of such discriminate social learning in rats.

In light of results from experiment 1, the failure of observers in experiment 2 to behave as theory would predict, instead adopting the diet preferences of ill and healthy demonstrators with equal probability, suggests that observers' internal state prior to interacting with demonstrators affected their probability of attending to the success of potential demonstrators. The delayed gastrointestinal upset, experienced by observers in

experiment 1 after eating diets ani and cin, was intended to make them uncertain with regards to the relative safety of these two foods. Observers, in experiment 2 did not become ill after eating the novel foods and therefore had personal knowledge that the foods were safe.

Taken together, results of these two experiments indicate that rats discriminate between successful and unsuccessful demonstrators, but do so only when they are uncertain, and the social information provided by demonstrators is relevant to the source of observers' uncertainty. Although certain and uncertain observer rats were tested for discriminate social learning in distinct experiments, we went on to analyze the data together, however, the interaction between observer certainty and demonstrator success was not significant (Repeated Measures ANOVA, with arcsine square root transformation, $F_{1,140} = 2.47$, $P = 0.12$). Ideally, experiments 1 and 2 would have been conducted at the same time to permit random assignment of subjects to conditions and to prevent any weakening of the interaction resulting from uncontrolled differences in conditions prevailing when the two experiments were run.

Nevertheless, the data presented in Figures 1 and 2 are consistent with our hypothesis that interactions exist between the copy-when and copy-who strategies of social learning. Possibly, previous experiments that explicitly tested other copy-who strategies and failed to find supporting evidence may not have constructed scenarios in which observers' internal state would predispose them to be discerning copiers. For example, Galef and Whiskin (in press) reported that rats were marginally more likely to copy unfamiliar, non-kin than familiar kin. Perhaps, if the observers had been uncertain

when they interacted with their demonstrators, they would have showed the discriminate social learning that theory predicts.

In sum, we suggest that further investigation of interactions between copy-when and copy-who strategies is a promising approach to both empirical and theoretical studies of social learning.

APPENDIX

In an effort to investigate potential interactions between *copy-when* and *copy-who* strategies of social learning, I conducted two other experiments in addition to those presented in the main body of this thesis. Both of the following experiments addressed the copy-who strategy *copy-successful-individuals* and, in experiment 4, I again integrated it with the *copy-when-uncertain* strategy, though the protocol was different from that of experiment 1. In experiment 3, I sought to determine if observer rats would copy successful individuals when *individual-learning-is-costly*. Neither experiment lends empirical support to our hypothesis that interactions exist between copy-when and copy-who strategies that elicit the use of discriminate social learning by observer rats.

GENERAL METHODS

The experiments presented this thesis shared the same general premise and basic methodology, with specific parameters being unique to each study. In each case, we first constructed an experimental setting that constituted a *copy-when* situation for observer rats, and afterwards presented observers with successful and, or unsuccessful demonstrators, thus providing observers with a *copy-who* situation. Control observers similarly experienced the *copy-who* situation though without having experienced the preceding *copy-when* treatment. The more detailed methodology outlined below is most relevant to experiments 3 & 4, in which observers interacted simultaneously with successful and unsuccessful demonstrators.

Subjects

Experimentally naïve, 8- to 9-week-old, female Norway rats (*Rattus norvegicus*), obtained from Charles River Canada (St. Constant, Quebec), served as observers. We randomly assigned observers to treatment and control groups and likewise assigned additional female rats, that were observers in previous social learning experiments, to serve as successful and unsuccessful demonstrators when 10- to 11-weeks old. We used each demonstrator twice, so that each demonstrator interacted with two different observers (one per day for 2 consecutive days). On the second day of interactions, each demonstrator ate the opposite diet from that which it had eaten on the first day.

Apparatus

For the duration of the experiment, we housed rats individually in stainless-steel hanging cages (35 x 18 x 21 cm) where they had ad libitum access to water. We provided rats with food in semi-circular, stainless-steel food cups measuring 10 cm in diameter, 5cm in depth.

Diets

We prepared diets by mixing powdered Diet 8640 (Harlan-Teklad, Madison, Wisconsin, U.S.A.) with 3 spices: marjoram, anise and cinnamon (hereafter called diet mar, diet ani and diet cin, respectively). Ground marjoram and anise were purchased from The Horn of Plenty (Dundas, Ontario, Canada) and we used McCormick's ground cinnamon (McCormick Canada, London, Ontario).

General Procedure

Step 1: Food deprivation

To ensure that observers and demonstrators would eat at a specific time on the test day, we put them on a feeding schedule during which time we fed them powdered Diet 8640 for 1 hr/day for 3 consecutive days.

Step 2: Observer treatment – “Copy when”

The main difference in protocol that distinguishes experiment 3 from experiment 4 occurs in step 2. Here, I outline the general concept but the detailed reports of this step for each experiment are presented later.

After a few days of training, once the rats had become accustomed to the scheduled feeding, observers in the treatment group experienced experimental conditions that constituted a particular *copy-when* scenario. Meanwhile, control observers experienced experimental conditions that, as much as possible, mirrored those of the treatment group but differed in a fundamental way such that they did not constitute a copy-when situation. During this time, we fed the demonstrator rats according to schedule.

Step 3: Demonstrator treatment – “Copy who”

We distinguished successful from unsuccessful individuals by injecting unsuccessful individuals intraperitoneally with a 0.13 M lithium-chloride (LiCl) solution immediately after they ate a novel food, whereas successful individuals received no such injection after

eating. As a result, the unsuccessful demonstrators endured a transient bout of gastrointestinal upset, including diarrhea, lasting approximately 15 min and from which they quickly and fully recovered.

On the day following step 2, for 1 hr we gave half of the demonstrators assigned to the successful and unsuccessful conditions a weighed food cup of diet ani and the remaining demonstrators in each group a weighed food cup of diet mar. At the end of 1 hr, we removed and weighed the food cups to make certain that each demonstrator ate a minimum of 3.0 g. We then injected each demonstrator assigned to the unsuccessful condition with the LiCl solution, equivalent in volume to 1% of its body weight.

Immediately following injection, we placed one successful and one unsuccessful demonstrator, one fed diet ani and the other diet mar, into the hanging cage of an observer and allowed the three rats to interact for 30 min. Assignment of diet ani and diet mar to demonstrators was counterbalanced so that, as a group, observers in both the treatment and control groups interacted equally often with unsuccessful demonstrators fed diet ani and diet mar and, consequently, successful demonstrators fed diet mar and diet ani.

Step 4: Food preference test.

After 30 min of demonstrator-observer interactions, we removed demonstrators and gave each observer two weighed food cups, one containing diet ani and the other diet mar. Ten and 23- or 24-hr later, we weighed both food cups and determined the percentage of the successful demonstrator's diet eaten by each observer.

EXPERIMENT 3: Copy successful individuals when individual learning is costly

The *copy-when-individual-learning-is-costly* strategy relates to Boyd and Richerson's (1985) costly information hypothesis in addressing the tradeoffs associated with acquiring accurate but costly information versus cheap but potentially less accurate information (Laland, 2004). Theory predicts that when personal information is too costly to acquire or make use of, then individuals should rely on relatively cheaper information provided by others (Boyd & Richerson, 1985). Social learning of antipredator behaviours in animals, for which there is much empirical support, clearly exemplifies this strategy (Chivers & Smith, 1995; Kelley et al., 2003; Mineka, S. Cook, M., 1988). In an experiment with guppies (*Poecilia reticulata*), Kendal et al. (2004) found that when relying on personal information was costly, which in this case meant losing visual contact with the shoal, guppies ignored their personal knowledge and instead relied on social information provided by foraging conspecifics, even when this information conflicted with an individuals' prior knowledge. Conversely, when relying on personal information was not costly (i.e. did not entail breaking away from the shoal), guppies used personal knowledge to guide their foraging decisions and ignored the available social information (Kendal, Coolen, & Laland, 2004). Similarly, Templeton and Giraldeau (1996) found that foraging European starlings (*Sturnus vulgaris*) relied more on social information to assess patch quality when information gained from individual learning was difficult to acquire, compared to conditions in which individual learning was easy. Therefore, when acquiring, or similarly relying on, personal information is costly, copying others is a viable alternate strategy.

In this experiment, I determined whether increasing the costs associated with individual learning would cause individuals to be more discriminating regarding from whom they learned when simultaneously presented with both a successful and an unsuccessful demonstrator. If the relative costs of individual learning affect the propensity to be more selective when choosing a model for social learning, then rats that have experienced experimentally induced toxicosis after eating a novel food should be more reliant than control rats (that have not experienced toxicosis after eating a novel food) on information provided by a successful than by an unsuccessful demonstrator.

Methods

Subjects

We randomly assigned 36 observers to the costly-individual-learning ($N = 18$) and control ($N = 18$) conditions. An additional 36 female rats served here as successful ($N = 18$) and unsuccessful ($N = 18$) demonstrators.

Diets

We prepared diet mar, diet ani and diet cin by adding, respectively, 2%, 1% and 1% by weight of each spice to Diet 8640.

Procedure

Step 2: Observer treatment – “Copy when”

On the 4th day of scheduled feeding, for 1 hr we gave observers a weighed food cup containing diet cin. After 1 hr of feeding, we weighed the food cups to ascertain that each observer ate a minimum of 3 g of diet cin and then injected each observer assigned to the costly-individual-learning condition intraperitoneally with a 0.13 M lithium-chloride (LiCl) solution, equivalent in volume to 1% of its body weight. Observers in the control condition received an injection containing an equivalent amount of isotonic saline. We then left the observers undisturbed for 24 hr, with ad lib access to water.

Results and Discussion

We removed one observer from the experiment because it failed to eat 3.0 g during Step 2.

Contrary to our prediction that the treatment observers would eat more of their healthy demonstrators' diets than control observers, over the entire 24 hr period, the treatment observers ate less of their healthy demonstrator's diet than control observers (Student's *t* test with arcsine transformation: $t_{1,33} = -2.16$, $P < 0.038$). The difference between groups was most apparent during the first 10 hr of the test (Student's *t* test with arcsine square root transformation: $t_{1,33} = -2.55$, $P < 0.015$; Fig. 3). However, there was no difference in the proportion of healthy demonstrators' diet eaten by observers during the 10- to 24-hr period (Student's *t* test, not assuming equal variance; $t_{1,31.4} = 0.49$, $P > 0.63$; Fig. 3). Moreover, the difference between groups is not significant when both 10-

and 24-hr intakes are included in one model (Repeated Measures ANOVA with arcsine square root transformation: $F_{1,31} = 1.88, P > 0.18$). Nevertheless, looking at Figure 3, the difference between treatment and control observers during the first 10 hr period suggests that observer's experience prior to interacting with healthy and ill demonstrators does affect observers' food preferences, at least in the short term.

Observers assigned to the treatment and control conditions ate equal amounts of food during testing (mean \pm SEM: costly-individual-learning observers: 23.8 ± 0.5 g ; control observers: 24.1 ± 0.6 g; Student's t test: $t_{1,33} = 0.41, P = 0.68$). All observers ate significantly more food during the first 10 hr of testing than during the 10- to 24-hr period (Repeated Measures ANOVA: $F_{1,31} = 246.70, P < 0.0001$) but there was no difference in temporal eating patterns between poisoned and control observers ($F_{1,31} = 0.29, P = 0.59$). Unfortunately, in spite of preliminary palatability tests conducted to ensure that observers would find both diets equally attractive, during testing all observers ate more diet ani than diet mar (mean percent \pm SEM diet ani of total food eaten: $57.2 \pm 2.5\%$; one sample t test: $t_{1,34} = 2.87, P < 0.007$). However, there was no difference between treatment and control observers in diet preference, precluding the possibility that observers' pre-conditioning during step 2 influenced subsequent diet choices (Student's t test with arcsine square root transformation: $t_{1,33} = -1.61, P = 0.25$).

While the proportion of healthy demonstrator's diet eaten by both treatment and control observers did change over the course of the 24-hr test, it can be argued that the first recording at 10 hr is the most important regarding questions of social learning, as observers' subsequent individual learning, via repeated sampling of both food types,

verified that both diets were safe to eat and did not produce illness. Therefore, when simply looking at the data collected at 10 hr, our hypothesis that increasing the costs of individual learning would cause observers to exhibit discriminate social learning is not supported by the data, as treatment observers ate both healthy (successful) and ill (unsuccessful) demonstrators' diets indiscriminately (mean percent \pm SEM healthy demonstrator's diet eaten 1 to 10 hr: $44.5 \pm 4.5\%$; one sample t test: $t_{1,16} = -1.22$, $P > 0.24$; Fig. 3). Unexpectedly, not only did control observers eat a greater proportion of their healthy demonstrators' diets than treatment observers, control observers ate significantly more of the healthy demonstrator's than would be predicted by chance (1 to 10 hr: $60.9\% \pm 4.5$; one sample t test: $t_{1,17} = 2.44$, $P < 0.03$; Fig. 3).

Neither treatment nor control observers had previously encountered diet ani or diet mar and were therefore unfamiliar with both foods. In failing to take this into consideration, we unintentionally introduced a degree of uncertainty into the experiment that may have affected the results. Why control observers, but not poisoned observers, would exhibit discriminate social learning is not clear. However, in light of the observers' taste preference for diet ani and the confounding uncertainty factor introduced by our protocol, it is difficult to draw any conclusions. Therefore, we chose to further examine the discriminate social learning demonstrated here by the control observers in a follow up experiment.

EXPERIMENT 4: Copy successful individuals when uncertain

We conducted the following experiment to determine whether rats selectively rely on socially acquired information when uncertain about the relative safety of two foods. Though similar in principle to experiment 1, experiment 4 is different in that it resembles a situation rats are likely to encounter more frequently in nature. More specifically, the costs of relying on individual learning are explicit in experiment 1 as observer rats know from experience that one (or both) of the novel foods causes illness, whereas the costs of uncertainty in the present experiment are implicit in simply encountering novel foods.

We predicted that if uncertainty causes an individual to be more discriminating when adopting socially acquired food preferences, then rats presented with two novel foods should rely more on food-related information provided by a successful demonstrator than by an unsuccessful demonstrator, compared to control rats that are presented with two familiar foods.

Methods

Subjects

We randomly assigned 24 observers to certain ($N = 12$) and uncertain ($N = 12$) conditions. An additional 24 female rats served here as successful ($N = 12$) and unsuccessful ($N = 12$) demonstrators.

Diets

We prepared diet ani and diet mar by mixing powdered diet 8640 with 1% by weight ground anise and ground marjoram, respectively. We added 1% by weight

granulated white sugar to diet mar so that the rats would find both diets equally palatable (Redpath Sugar Ltd., Toronto, Ontario).

Procedure

Step 2: Observer treatment – “Copy when”

On the 4th day of scheduled feeding, we gave each observer assigned to the uncertain condition a weighed food cup that contained powdered Diet 8640 for 24 hr. At the same time, we provided each observer in the certain condition, for 24 hr, with two weighed food cups that contained diet ani and the other diet Mar. After 24 hr, we removed the food cups and weighed them ascertain that each observer assigned to the certain condition ate a minimum of 1.0 g of each diet, and that observers assigned to the uncertain condition ate a minimum of 2.0 g of powdered Diet 8640. Any observer that failed to eat its minimum food consumption requirement during the 24 hr period was removed from the experiment.

Results and Discussion

We removed two observers from the experiment because they failed to eat a minimum of 1.0 g of each diet ani and diet mar during step 2 of the experiment.

Contrary to our hypothesis that uncertain observers would prefer the diet of their healthy demonstrator, observers assigned to both certain and uncertain conditions ate similar proportions of their healthy demonstrators' diets (Repeated Measures ANOVA with arcsine square root transformation: $F_{1,18} = 0.42$, $P = 0.53$; Fig. 4). Observers

assigned to both certain and uncertain conditions also ate equal amounts of total food during the test (Repeated Measures ANOVA: $F_{1,18} = 1.38, P = 0.25$). All observers ate significantly more during the 10- to 23-hr period than during the first 10 hr (Repeated Measures ANOVA: $F_{1,18} = 79.85, P < 0.001$), which is not surprising given that all observers were likely satiated as they had had ad libitum access to food for 24 hr prior to the food preference test.

Interestingly, during the entire 23 hr food preference test, the proportion of healthy demonstrators' diets eaten by all observers was *less* than would be predicated by chance (mean proportion healthy demonstrator's diet eaten \pm SEM: $39.0 \pm 4.9\%$; one sample t test: $t_{1,21} = -2.26, P < 0.034$). This preference for ill demonstrators' diets cannot be easily explained, and yet Galef et al. similarly found that observers exhibited a non-adaptive preference for poisoned demonstrators' diets after simultaneously interacting with both poisoned and unpoisoned demonstrators (Galef et al., 1990). One possible explanation is that ill demonstrators are relatively inactive and observer rats therefore have more opportunities to smell the breath of ill than healthy demonstrators. However, our lab recently falsified this hypothesis and, though intriguing, pursuing this issue was beyond the scope of my thesis (Dukas & Galef; unpublished data).

Unlike experiment 1, in which uncertain observers preferred the diets of successful demonstrators, the results of the present experiment do not support our prediction that uncertainty causes individuals to be more discriminating when choosing whom to copy from successful and unsuccessful demonstrators.

CONCLUSIONS

For reasons discussed above, I cannot unambiguously draw any conclusions from experiment 3. The results of experiment 4 also do not lend support to our hypothesis that interactions exist between copy-when and copy-who strategies that predispose individuals to be more discriminating when choosing whom to copy. Nonetheless, the data from experiments 1 & 2 clearly demonstrate that Norway rats are capable of discriminate social learning, and that uncertain rats preferentially copy successful individuals.

Experiments 1 and 4 both examined the effects of uncertainty on observer rats' propensity to discriminate between successful and unsuccessful demonstrators, and there are a couple reasons that may explain why experiment 1, but not 4, supported our prediction. First, as previously mentioned, the costs of uncertainty were explicit in experiment 1 as observers knew from personal experience that one or both of the diets they ate caused illness whereas, in experiment 4, the cost of uncertainty were implicit in simply encountering novel foods. To be more precise, the uncertainty we created in experiment 1 was manifest in observers' experience, while the uncertainty we created in experiment 4 was manifest in the *absence* of observers' prior experience. While rats are naturally neophobic, this reluctance to ingest novel foods may not have been sufficiently salient to cause observer to attend to the quality of demonstrators. Second, observers in experiment 4 interacted simultaneously with two demonstrators, each having recently eaten a different food, whereas observers in experiment 1 encountered a single demonstrator that provided information regarding a single food-type. It is possible that observers that interacted with two demonstrators, and received information regarding two

food-types, were over-stimulated and consequently failed to distinguish between the relative health of their respective demonstrators. The doubling of social information communicated by demonstrators, in conjunction with the implicit costs of uncertainty, may have effectively eradicated rather than elicited the use of discriminate social learning by observers in experiment 4.

Despite the failure of the experiments 3 and 4 to support our hypothesis, the data presented in experiments 1 & 2 are robust and indicative that interactions between copy-when and copy-who strategies can elicit the use of discriminate social learning, specifically with regards to uncertainty and the relative success of prospective demonstrators.

To conclude, the work presented in this thesis provides the first clear evidence of discriminate social learning in Norway rats and likewise demonstrates that *copy-successful-individuals* is a viable strategy in this species. More importantly, however, in examining interactions between copy-when and copy-who strategies, we have introduced a new and promising approach to the study of social learning.

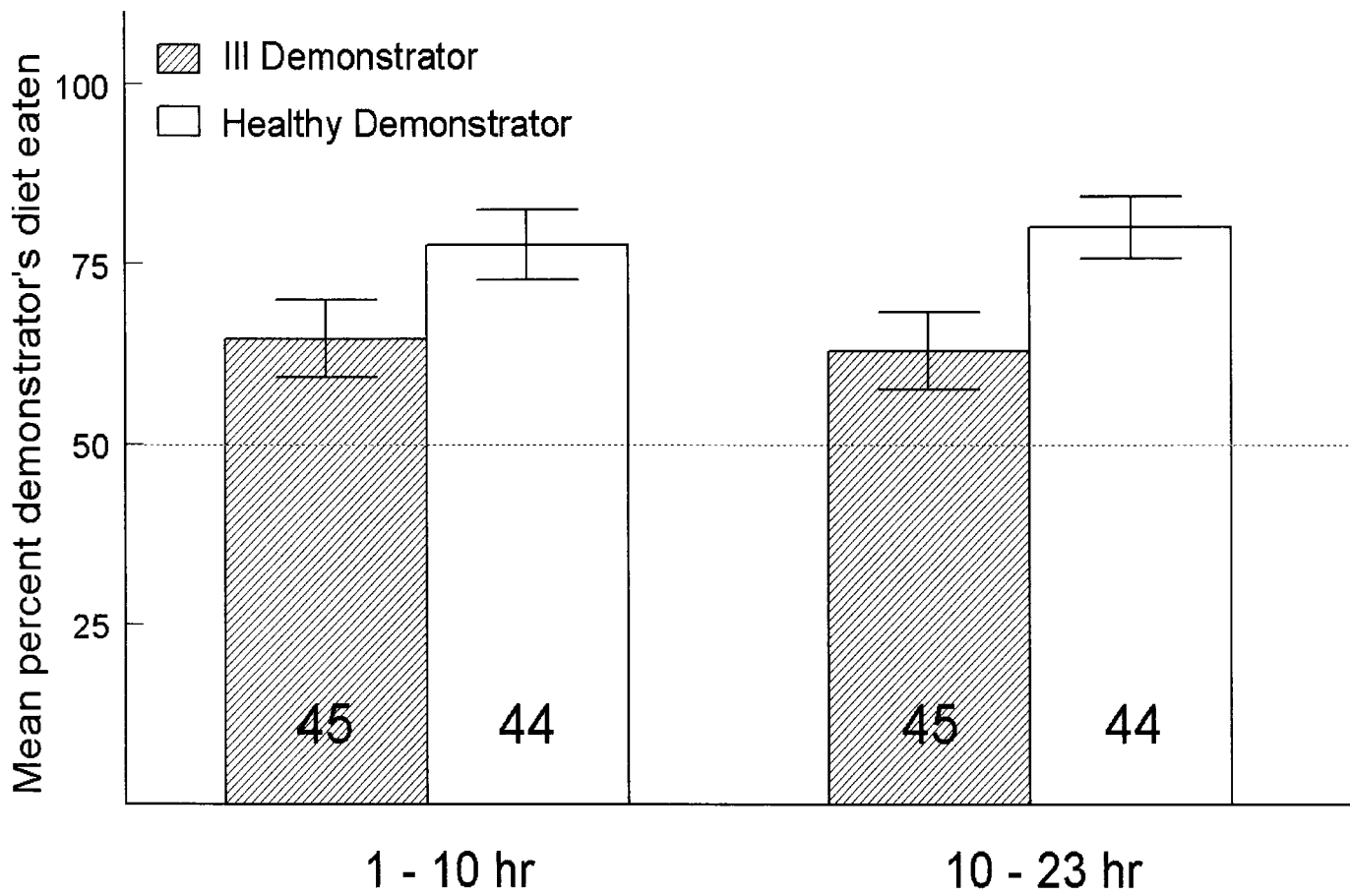
Figure Captions

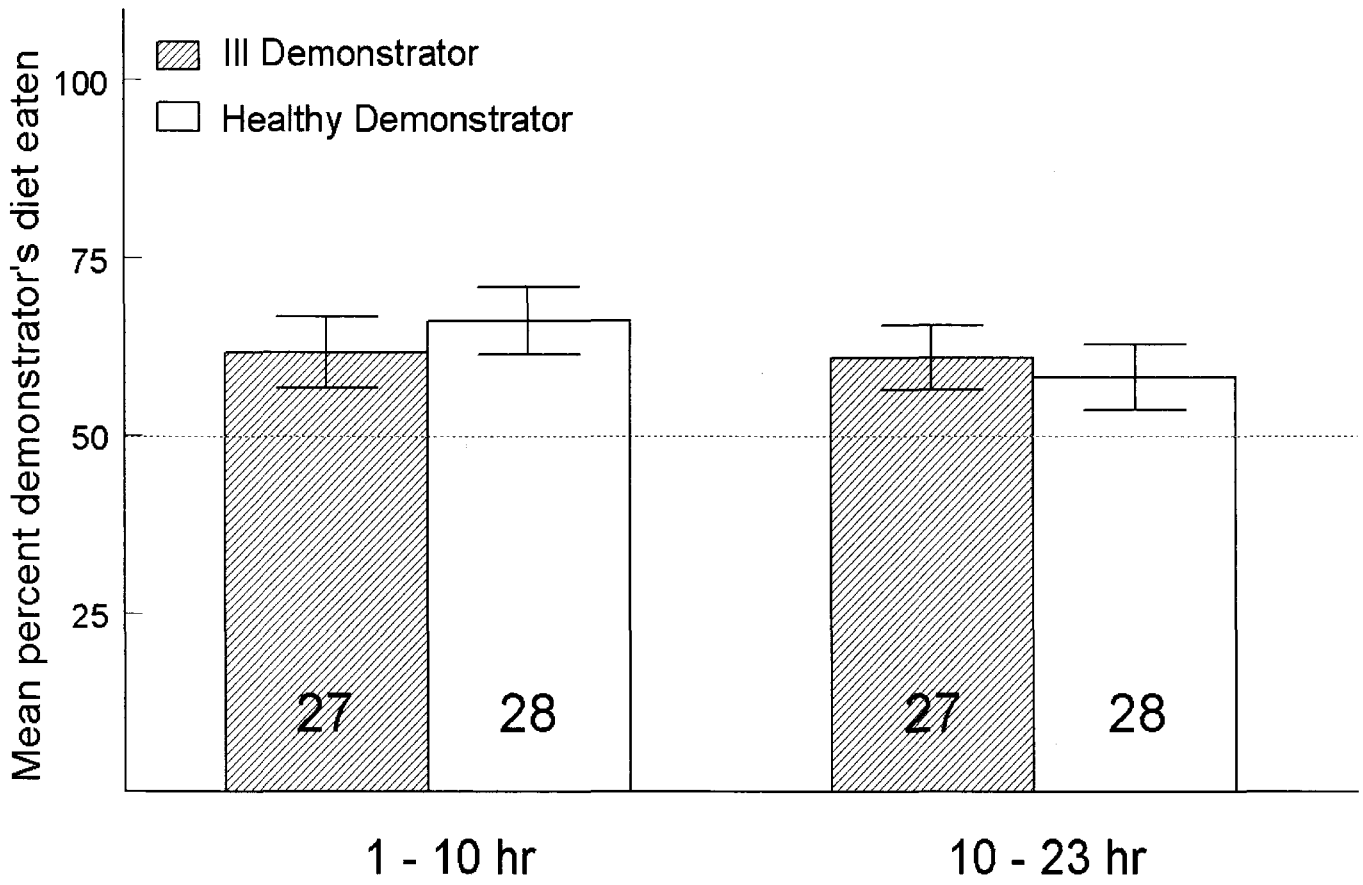
Figure 1: Mean (± 1 SEM) percent of demonstrator's diet eaten by uncertain observers that had interacted with either ill or healthy demonstrators in experiment 1. Numbers inside histograms = N per group.

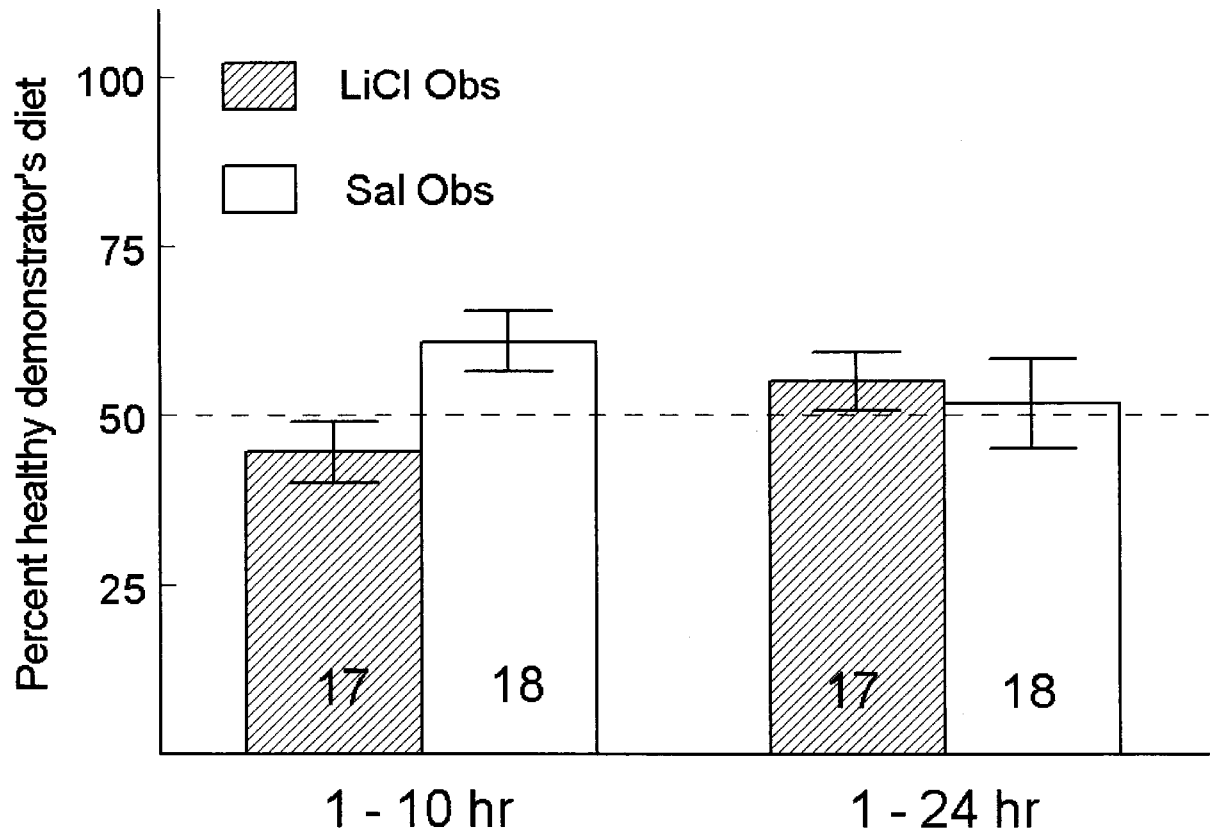
Figure 2: Mean (± 1 SEM) percent of demonstrator's diet eaten by certain observers that had interacted with either ill or healthy demonstrators in experiment 2. Numbers inside histograms = N per group.

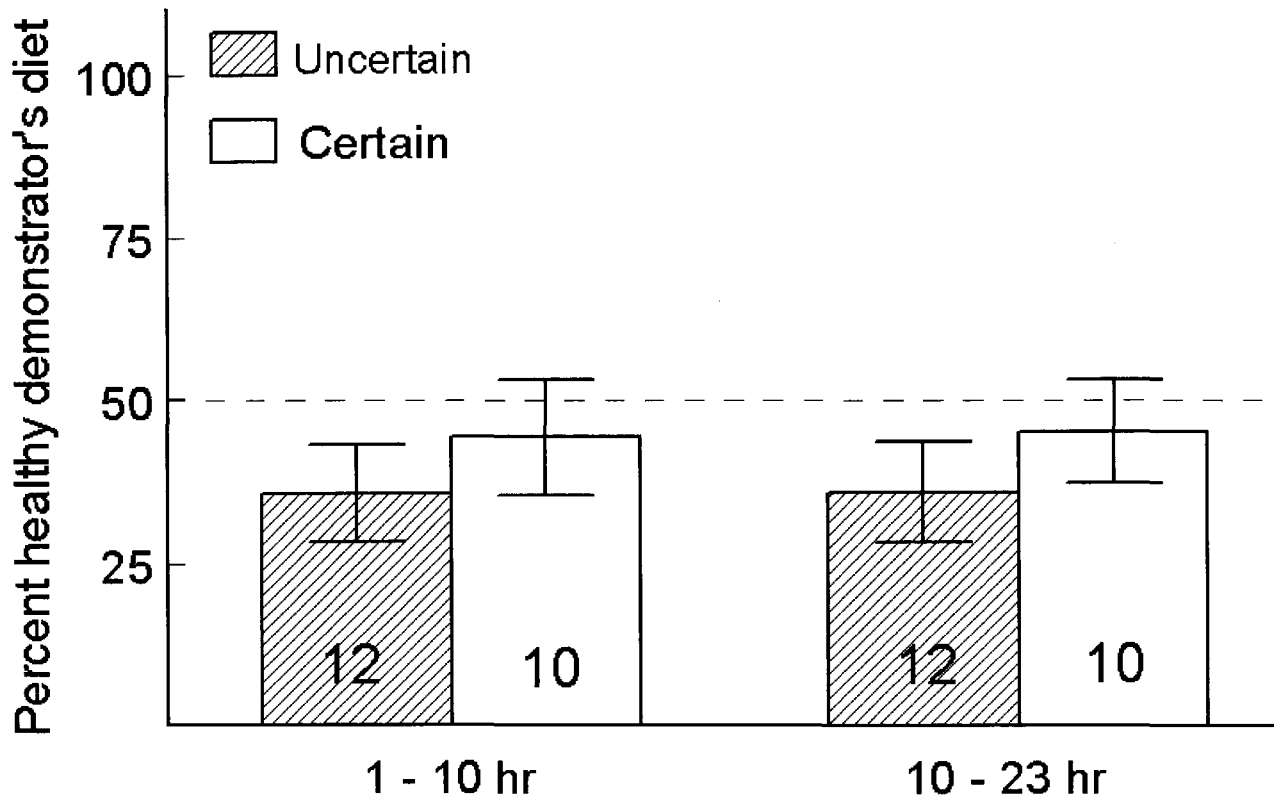
Figure 3: Mean (± 1 SEM) percent of healthy demonstrator's diet eaten by observers whose prior personal learning experience was either costly (LiCl Obs) or not (Sal Obs). Numbers inside histograms = N per group.

Figure 4: Mean (± 1 SEM) percent of healthy demonstrators' diets eaten by certain and uncertain observers. Numbers inside histograms = N per group.









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