Evidence for Enhanced Learning of a Socially Transmitted Food Preference in Rats Interacting in Large Groups

Carla L. Lipscombe

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ABSTRACT

Evidence for Enhanced Learning of a Socially Transmitted Food Preference in Rats Interacting in Large Groups

Carla Lipscombe

Socially Transmitted Food Preferences (STFP) are typically assessed in laboratory rats by allowing a *single* Observer to interact with a Demonstrator fed a distinctly flavored food. Social learning is gauged by the Observer rat's subsequent preference for the Demonstrator's diet to equally palatable alternatives. This thesis tested the hypothesis that modifying the design of conventional protocols to better match the conditions that would underlie STFP in a rat's natural habitat will enhance laboratory-assessed social learning. In Experiment 1, the ability for *multiple* Observers interacting simultaneously with a single Demonstrator to acquire a food preference was assessed. Rats were reared for 10 weeks in enriched housing conditions and tested under conventional (CL) or group-learning (GL) approaches. The results revealed a greater tendency for GL rats to consume their respective Demonstrators' diets than CL rats. Observers tested under CL failed to display a food preference. In Experiment 1B, the influence of impoverished rearing conditions on STFP was assessed. Rats were reared under standardized housing conditions and tested using CL. Impoverished rats acquired a more robust preference when rearing conditions and learning conditions were more similar. In Experiment 2, the role of the hippocampus in the acquisition and retention of STFP under GL was assessed at 10 min following the learning phase. Rats receiving hippocampal lesions performed similarly to sham lesion rats and consumed more of the

diet eaten by their respective Demonstrators. In sum, these results provide support for enhanced learning of food preferences under semi-naturalistic conditions.

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Socially transmitted food preferences (STFP) are produced in laboratory rats by feeding a 'demonstrator' rat a novel flavored food and then allowing it to interact with an experimentally naïve 'observer' rat for a brief period of time. Subsequently, the observers tend to prefer the novel flavour eaten by the demonstrator over a different novel flavour presented concurrently (Galef & Wigmore, 1983). STFP has been found to be exceptionally resistant to parametric variation, suggesting an important role for this form of learning in guiding the feeding behavior of free-roaming wild rat populations. Presumably, STFP would function to permit opportunistic feeders, such as rats, to make use of public information so as to expand their repertoire of safe and edible foodstuffs, while reducing the risk associated with individual trial and error learning about novel prey (e.g. ingestion of toxins) (Galef & Giraldeau, 2001). However, due in part to a lack of field studies on the subject, the role of STFP in guiding the feeding behavior of feral rats is uncertain. For example, in the conventional paradigm, social learning occurs during interaction between a single demonstrator rat and a single observer, within the confines of a small enclosure. However, when a feral rat returns to the colony following a foraging expedition, it has the opportunity to interact with several colony mates.

The main aim of the experiments reported in this thesis was to determine whether food preferences are acquired when multiple observer rats interact with a single demonstrator concurrently, within a large enclosed space. Secondary aims included;

1) comparing the reliability of social learning in the multiple-observer setting with that which occurs in the conventional approach (a single observer interacting with a Demonstrator within a small space)

2) assessing the effects of environmental enrichment during development on the later acquisition or expression of STFP in adult rats

3) determining whether damage to the hippocampal formation disrupts STFP learning

Experiment 1A was undertaken to determine whether the use of semi-naturalistic testing procedures would facilitate the acquisition of a food preference by multiple Observer rats interacting simultaneously with a single Demonstrator.

To test this prediction, rats were given daily exposure to enriched environments from post-weaning until the age of 13 weeks and were tested as adults in one of two ways. In the *conventional-learning* approach, Observers and Demonstrators interacted one on one within the confines of a small shoebox cage. In the *group-learning* approach, groups of Observer rats ($n \geq 10$ per group) interacted simultaneously with one pre-fed Demonstrator in a large multi-level complex environment.

The main finding was that subjects in the group condition ate proportionally more of the demonstrator-matched diet than did subjects that had learned the information via the conventional approach, suggesting that under conditions more akin to those found in a rats natural habitat, social learning is facilitated.

Experiment 1B was undertaken to determine whether the enriched rearing conditions that rats from Experiment 1A experienced throughout development influenced their ability to acquire a food preference in adulthood.

To test this hypothesis, rats were reared under standard housing conditions and tested under the conventional protocol. At no time did this group of rats receive exposure

to environmental enrichment during development. The main finding was that rats housed under impoverished conditions acquired a food preference that was greater in magnitude than food preferences acquired by rats raised under enriched conditions and tested under conventional protocol.

Experiment 2 was undertaken to assess the effects of hippocampal lesions on the acquisition and expression of a food preference under the group-learning protocol.

Rats received either sham or hippocampal lesions prior to testing. Following a short recovery, all rats were tested under group-learning conditions, with a 10 min interval between the learning and test phase. The main finding was spared performance in hippocampal-lesion rats relative to sham-lesion rats.

Overall, the findings of this thesis suggest that multiple Observer rats interacting simultaneously with a single Demonstrator can acquire a food preference evident up to 24 hr following the learning phase. As well, by tuning laboratory test environments to better match the conditions that would support this naturally occurring form of learning in a rat's natural habitat, social learning by rats tested under group protocol was enhanced relative to the performance of rats tested under conventional protocol. Furthermore, the results from Experiment 2 provide preliminary evidence for an interaction between rearing conditions and the ability to acquire or express a socially transmitted food preference.

The following introduction and literature review is divided into 5 main sections. Section 1.2 reviews the literature on STFP with a focus on the conventional paradigm and the insights we have gained from decades of laboratory based research. Section 1.3 discusses the ecological significance of STFP in rodents. Section 1.4 describes research

on the effects of environmental enrichment as it pertains to learning. The issue of standardized housing and its effects on learning in the laboratory are discussed. Section 1.5 reviews the literature on the effects of hippocampal damage on STFP in rodents.

1.2 What we have learned about STFP from laboratory research

The behavior of animals can be affected in both subtle and dramatic ways by the presence of a conspecific. In certain cases, the effect of a social encounter is to simply increase the frequency or likelihood that an animal will perform a behavior already in its own repertoire. A common manifestation of this form of 'social enhancement' is yawning in humans, or the grazing behavior of cattle and horses. In contrast to 'social enhancement', 'social learning' is a descriptive term reserved for instances where exposure to a behaving conspecific results in the acquisition of a novel behavior pattern on the part of the observer, that extends beyond the period of the interaction, and can be expressed in the absence of the demonstrator. Unlike social enhancement, socially learned behaviors involve the adoption of novel forms of behavior not present in the observers original repertoire (Galef, 1988, p. 13). For example, red-winged black birds will acquire a preference for a particular food over a second one of equal palatability that a fellow conspecific has been seen eating (Mason, 1988, p. 99; Mason, Artz & Reddinger, 1984). A striking example of social learning occurs among foraging members of honeybee societies. Upon return from a foraging expedition, honeybees will perform a 'waggle dance' on the vertical surface of the hive wall so as to 'inform' other honeybees as to the location and distance of a nectar source (Gould, 1975).

In one form of social learning in rodents, a naive rat ('observer'), following a social encounter with a recently fed conspecific ('demonstrator') will come to prefer that flavor smelled on the breath of the demonstrator over a second novel flavor presented concurrently. The social transmission of food preferences (STFP) is presumed to benefit wild, free roaming rat populations by expanding their knowledge of safe foods in their environments, thereby reducing the likelihood of consuming toxic foods; a risk associated with individual trial and error learning (Galef & Wigmore, 1983).

STFP is reproduced in laboratory rats by pre-feeding a demonstrator rat one of two novel diets and then allowing it to interact (in the absence of the diet) for a brief period of time with a single, experimentally naïve observer rat. Following the interaction phase, and, in the absence of the demonstrator, the observer rat is offered a choice between the two diets. The classic finding is that the observer rat exhibits an enhanced preference for the diet consumed by the demonstrator rat (Galef & Wigmore, 1983; Posados & Andrews, 1984; Strupp & Levitsky, 1984).

Early laboratory based research on STFP revealed that the simple act of exposing a rat to a particular diet in the absence of a conspecific did not result in a similar alteration of food preferences (Galef, Kennett & Stein, 1985). This finding ruled out the explanation that the observed influence of demonstrators on the food choice of observers was the result of demonstrator-induced familiarity with one diet relative to the alternative diet. Rather, it appeared that observer rats had to experience a diet within the context of stimuli provided by the presence of a conspecific, suggesting the phenomenon reflected the operation of social learning processes.

Early attempts to decipher the critical features of the context or signals supporting the acquisition of a food preference by observer rats revealed a role for 'diet cues' emerging from the anterior end of live demonstrator rats (Galef & Stein, 1985). If demonstrator and observer pairs were kept separated by a sheet of Plexiglas during the interaction phase, or if observer rats were rendered anosmic prior to the interaction phase, the transmission of food preferences did not occur (Galef & Wigmore, 1983; Galef, 1988).

However, the finding that interaction with either a surrogate rat, the anterior end of a dead rat, or the hind end of a live rat, also interfered with the acquisition of a food preference suggested that specific details of the context provided by the demonstrator rat (and not just the presence of the demonstrator) were necessary for STFP to occur (Galef & Stein, 1985).

In an effort to identify this contextual component, researchers first turned to the chemical analysis of the constituents of rat breath. Samples of air taken from the nasal cavity of live rats revealed the existence of significant quantities of the chemical carbon disulfide (CS_2) (Galef, Mason, Preti & Bean, 1988; Mason, Bean & Galef, 1988). Evidence that this chemical provided the necessary contextual cue was confirmed by behavioral analyses. Exposing an observer rat to a surrogate rat moistened with carbon disulfide and a powdered food was found to alter diet preferences, whereas a similar enhancement of preference failed to occur in rats exposed to a surrogate moistened with distilled water (Galef et al., 1988). Collectively, these findings suggest that both olfactory cues (provided by the food) and a rat-provided chemical context (carbon disulfide) are

necessary for the successful transmission of food preferences in laboratory rats (Galef, 2001).

Two decades of research has revealed STFP to be an exceptionally robust social learning phenomenon that is readily reproduced under a wide array of parametric variation. The basic procedure has been repeated using: old and young demonstrators, male and female observer/demonstrator pairs, familiar and unfamiliar observer pairs, replete and hungry observers and liquids for ingestion rather than foods. In each case, an enhancement of food preferences has been observed (Galef, Kennett & Wigmore, 1984; Galef, Rudolf, Whiskin, Choleris, Mainardi, Valsecchi, 1998). In an illustration of the stability and robust nature of STFP, Galef provided observer rats with a series of potentially disruptive food-related events during a 6-day interval between the acquisition of a food preference and the test phase. During the intervening period, observer rats were given daily exposure to either a demonstrator rat that had consumed a separate novel diet, daily access to other novel diets or both daily access to other diets and interaction with a demonstrator rat fed those diets. In each case, observer rats retained the original preference learned despite exposure to 6 days of intervening events (Galef, Lee & Whiskin, 2005). While rats in this experiment were only tested for food preferences acquired during their original encounter, it is conceivable that they learned more than one food preference throughout the 6-day period. In fact, it appears that rats are quite adept at identifying and utilizing multiple messages from a single demonstrator fed a mixture of up to four distinctly flavored diets (Galef & Whiskin, 1992).

Observer rats can also extract and store information from up to four different conspecifics, each having consumed a distinct diet (Galef, 1983). These preferences are

subject to change as observers are exposed to different demonstrators having eaten different diets on separate days over a 2 week period (Galef, Attenbourough & Whiskin, 1990, Galef & Whiskin, 2000).

STFP is exceptionally resistant to the passage of time. Up to 4 hr following ingestion of a particular food, demonstrators continue to emit cues sufficient for transmission of a preference for that food (Galef & Kennett, 1985). Furthermore, information acquired during even a single brief exposure (15 min) can alter food preferences up to one month following the interaction phase (Galef & Whiskin, 2003). The findings from one study provide evidence for very little forgetting of a socially induced preference 3 months following a single 10 min exposure (Clark, Broadbent, Zola & Squire, 2002). Such food preferences are not permanent however. For example, with continued exposure to alternative diets, the stability of an acquired preference wanes (Galef & Whiskin, 2001). This effect is likely the result of a decrease in the neophobic response towards the alternative diet as opportunities for asocial learning about it increase (Galef & Whiskin, 1997). These data suggest that socially acquired information and individual learning can interact in meaningful ways to shape food selection in rats. Laboratory research has shown that rats with previous experience with a particular food are resistant to socially acquired food preferences for a brief duration (Galef & Whiskin, 1994). In a dramatic example of this transitory, inhibitory effect, Galef allowed observer rats to interact with a demonstrator fed a mixture of two diets. Rather than two completely novel diets, observer rats were given extensive prior experience with one of the diets. Being conservative feeders, one might predict that during the two-choice preference test following the interaction phase, observers would select the more familiar

diet for consumption over the second novel, potentially toxic diet. Interestingly, the effect of the social encounter was to enhance rat's preferences for the unfamiliar diet rather than the familiar alternative (Galef, 1993).

The finding that rats can identify foodstuffs other 'healthy' rats are eating and increase their consumption of those foods may lead some to question whether interaction with a 'non-healthy' conspecific will lead to rejection of a potentially 'toxic' diet. It is well known that rats readily learn to avoid tastes that have been associated with gastro-intestinal upset (Garcia & Koelling, 1966). This form of learning (taste-aversion learning) is considered an instance of Pavlovian conditioning, whereby a rat, following exposure to a flavour (conditioned stimulus), paired with illness (an unconditioned stimulus), develops an aversion to the flavour evidenced by behavioral avoidance and rejection upon subsequent exposure to it (conditioned response). The literature has demonstrated an important role for STFP in reversing previously learned taste aversions. For example, naïve rats, following interaction with a demonstrator fed a particular diet will exhibit a reversal of their aversion for that diet (Galef, 1985a; Galef, 1985b). Furthermore, observer rats fed two foods in succession and then poisoned, are more likely to avoid, upon subsequent exposure, whichever of the two diets they have not previously encountered on the breath of a conspecific (Galef, Laurel, McQuoid & Whiskin, 1990; Galef, 1987; Galef, Wigmore & Kennett, 1983). To investigate whether rats will acquire aversions as a result of interacting with a sick conspecific, investigators injected pre-fed demonstrator rats with the chemical compound lithium chloride (LiCl). Following an injection of LiCl, rats become ill and exhibit signs characteristic of systemic poisoning. During this period, observer rats were left to interact with demonstrators suffering the

effects of toxicosis. The results of the experiment revealed that Observers subsequently preferred the diet consumed by demonstrator rats (Galef, Wigmore & Kennett, 1983). The failure to find an aversion to the flavor that was paired with the sick demonstrator might be a reflection of the fact that demonstrator rats are simply an inadequate conditional stimulus (CS) for taste-aversion learning. To test this possibility, observer rats were made ill with an injection of LiCl either prior to or following the interaction phase with a healthy demonstrator. The result was a pronounced avoidance of the demonstrator-consumed diet when observer rats were made ill following exposure to the diet cue on the breath of demonstrators and not otherwise (Galef et al., 1983). Collectively these results show that rats do not acquire aversions to cues emitted by a conspecific suffering the effects of toxicosis, and that this failure is not due to the inadequacy of demonstrators as a CS for taste aversion learning.

However, there is support for socially transmitted aversions under certain conditions. For example, Gemberling (1984) has shown that mother rats will learn to avoid a novel substance ingested prior to the illness of her pups, whereas surrogate male rats and nulliparous females will not. Hishimura (1998) provides evidence that adult rats will learn to avoid a food when they have already acquired a weak aversion to that food and are subsequently exposed to a poisoned conspecific. This result confirms prior evidence suggesting a capacity for rats to identify a sick conspecific and a capacity for socially transmitted aversion learning in rats when they themselves are uncertain about a food's safety (Coombes, Revusky & Lett, 1980; Hishimura, 1998).

1.3 Ecological aspects of STFP

Free-living Norway rats are highly social, colonial animals that emerge from a central nesting site in search of food, water and bedding. Wild rats are considered 'opportunistic' feeders because they exploit a wide range of foods including plants, grain, seeds and nuts and small game such as fish and birds (Barnett, 2005, p. 15). As dietary generalists, rats are faced with the problem of having to compose nutritionally adequate diets from among the myriad of potential food sources, while avoiding the consumption of unfamiliar non-nutritive or toxic foods. Field observations of wild rat populations suggest that the diet choices of feral rats can be influenced by the presence and behavior of others in the colony. This was evidenced in the 1950's when pest control officers observed that poison baits placed within the home range of a colony that incurred initial success, became ineffective over time. Not only would members of the colony that survived the first round of poisoning subsequently avoid the bait, but the young born to surviving members rejected the bait as well (Galef & Clark, 1971; Galef, 1977, p. 126). These observations suggested that the feeding behavior of wild pups could be biased by the presence of elders and the dietary habits of adults could be modified by experience. Laboratory work has since demonstrated the existence of multiple behavioral processes that likely contribute to the development of adaptive patterns of food choice in both adults and pups. In the case of pups transitioning from a total dependence on milk to solid foods, survival is highly dependent on the efficient acquisition of appropriate foodstuffs for consumption. A number of response tendencies facilitate this task. For example, pups tend to trail adults to food sites, are more likely to initiate feeding at a site where adults have been feeding, and readily develop food preferences for foods found clinging

to the fur of elders as a result of simple exposure effects (Galef, 1977, p.126; Galef, 1990). Furthermore, rats, much like humans, have evolved congenital hedonic responses to certain substances. More specifically, sweet tasting substances, such as sugars, are generally readily accepted, whereas bitter tasting substances (which are often also toxic) tend to be avoided (Galef, 1996). Wild rats are highly neophobic with regards to certain kinds of stimuli, and will exhibit an extreme reluctance to consume novel foods and substances (Galef & Clark, 1971). This response tendency leads rats to feed on familiar diets that are likely safe rather than novel, potentially noxious diets. Additionally, rats tend to sample foods thereby minimizing the likelihood that they will consume a lethal dose of a toxic substance. In the case of accidental poisoning, rats that have survived the episode can associate the post-ingestional consequences of a suspect food (e.g. illness) with its flavor even hours following consumption. This one-trial learning results in the expression of powerful and long lasting aversions to toxic foods (Galef & Clark, 1971).

Much of the reputed cleverness of the wild rat can be attributed to the combined influence of each of these response tendencies. However, within such a behavioral complex, what added benefit would a social learning mechanism such as STFP provide the wild rat? Considered from an evolutionary perspective, it is thought that learning mechanisms are selected for in much the same way that any trait would be. Presumably, any trait that increases the reproductive fitness of its bearer over extant alternatives may come to be selected for over time through the process of natural selection. If STFP is an evolved capacity, what fitness benefits does it bestow upon its bearer?

For a cosmopolitan, dietary generalist such as the rat, colony members are a potentially valuable and convenient source of dietary information regarding both the

safety and location of foodstuffs. This is because selecting the same foods for ingestion as others in the colony is an efficient way to learn about what foods are safe to eat while avoiding the risk inherent in trial and error learning. Laboratory evidence has shown that rats are more likely to consume a novel unfamiliar food smelled on the breath of a conspecific than a familiar food (Galef, 1993). This finding suggests that a primary function of STFP is to motivate rats to expand their feeding repertoires to include unfamiliar foods that others are eating. In environments characterized by a seasonal cycle of food availability or during periods of food scarcity, information about the re-emergence of an old but familiar food source, or the safety of a novel foodstuff could be highly beneficial to the health and survival of any individual member of a colony, including the young, inexperienced, and less efficient forager.

A recent study suggests that in unstable environments, rats are less likely to use social information to guide their food choices. Following exposure to a conspecific fed a distinctly flavored food, observer rats were either maintained in a stable, predictable environment or were exposed to a highly variable one. In the latter case, observers were placed in a novel cage each day and fed at unpredictable times. During the test phase, the food choices of observers in the highly unstable environment were affected significantly less by the presence of a demonstrator than control rats maintained in stable conditions (Galef & Whiskin, 2003). In a highly variable environment, information carried on the breath of a foraging rat runs the risk of being outdated very quickly. In situations such as these, indiscriminately copying the behavior of others is unlikely to be an adaptive strategy, rather, relying on genetically coded information or asocial learning experiences to guide feeding is safer (Galef & Laland, 2005).

The inability of rats to learn to avoid foods that have made others in the colony ill may at first glance appear to be surprising. Other species of opportunistic feeders, such as the red-winged blackbird, can learn aversions to foods following a single exposure to a conspecific's adverse reaction to it (Mason, 1988, p. 99). However, in the case of the rat, there may simply be minimal selection pressures for such a capacity to evolve. For example, rats' innate adverse responses to bitter foods coupled with their strong neophobic response toward novel foods in combination with a capacity for one-trial taste aversion learning may provide ample protection against the ingestion of potential toxins (Galef, 1985).

Despite the lack of direct evidence for STFP in wild rats, there is convincing support for its use among a species of Australian mouse (*Mus domesticus)*. Much like rats, mice are social, central place foragers and can acquire food preferences from conspecifics. Furthermore, there appear to be a number of parallels with regard to the conditions that support the transfer of diet information in both species (Valsecchi & Galef, 1989). In their study, Valsecchi and colleagues trapped, maintained and tested groups of wild mice in large, outdoor, semi-natural enclosures. Under these conditions, demonstrator mice fed a novel food were able to influence the feeding preferences of up to 12, unrestricted, colony members (Valsecchi, Singleton & Price, 1996).

1.4 Environmental enrichment as a factor

It has been known for some time that rearing animals in 'enriched' environments as an alternative to standard laboratory housing promotes profound and long-lasting behavioral and neurobiological changes in a wide variety of species (Rozenweig &

Bennett, 1996).

The first formal study on the effects of differential housing on behavior started in 1947. Rats reared in 'free environments' (with frequently changing stimulus objects and spatial configurations) were shown to have superior learning abilities and performed significantly better as adults on a simple maze to food task (Hebb-Williams maze) than their 'impoverished' counterparts. This finding gave rise to the influential Hebbian concept of 'use-induced plasticity' of the nervous system (Rozenweig & Bennett,1996).

In the years to follow, evidence accumulated in support of an important role for the environment in the development of species-specific brain characteristics. For example, in a food-storing member of the crow family, early experience with caching food was found to be essential for the development of increases in hippocampal volume found in experienced others (Rozenweig & Bennett, 1996). In rodents, enriched housing has been associated with a host of changes in the cortex and hippocampal formation, including increases in cortical brain weights, neuron size, number of dendritic spines and dendritic branching, synapses per neuron, and excitatory synaptic connections; suggesting an increase in the processing capacity of the cortical regions concerned (Fernandez-Teruel, Gimenez-Llort, Escorihuela, Gil, Aguilar, Steimer, Tobena, 2002, Wurbel, 2001; Leggio, Mandolesi, Federico, Spirito, Ricci, Gelfo, Petrosini, 2005; Bennett, Rozenweig, Diamond, 1969). Collectively, these findings have led to the suggestion that early environmental stimulation may be necessary for the full growth of the brain and for the achievement of maximal behavioral potential (Rozenweig & Bennett,1996).

The finding that differential housing leads to improvements in cognition and changes in brain morphology gave rise to concerns regarding the usefulness of animals

housed in standard laboratory conditions as research subjects. Laboratory rodents in the behavioral neurosciences are typically reared under standardized housing conditions, characterized by small cages, low stimulation, and social deprivation. These conditions bear little similarity to the environment that would characterize the rat's natural habitat. The use of standardized housing is a widespread practice that remains prevalent despite the unnatural constraints it likely places on both behavior and brain development (Wurbel, 2001). Early proponents of the approach saw standardization as a means by which experimenters could decrease 'within-experiment' and 'between-experiment' variability (inter-individual variability) so as to facilitate the detection of effects and to increase the reproducibility of results (Wurbel, 2000). However, the act of imposing strict standards on test environments and housing practice can be problematic. For example, the push for high reproducibility increases the risk of detecting effects with low external validity (e.g. laboratory artifacts that are not generalizable to other conditions) or failing to detect effects with high external validity (Wurbel, 2000).

1.5 Role of the hippocampus in STFP

Investigations of the neural basis of STFP suggest an important role for the hippocampal formation (including dentate gyrus and subiculum). The preponderance of lesion studies assessing deficits in hippocampal-lesion animals report the normal acquisition and expression of food preferences when the learning phase is followed immediately by the test phase. Conversely, performance falls to chance levels when the learning and test phases are separated by longer delays of 24 to 48 hr (Clark et al., 2002; Bunsey & Eichenbaum, 1995). This suggests a critical role for the hippocampus in the

retrieval process but only at delays that are far beyond the duration of short-term memory memory. However, inconsistent results have been reported (Burton, Murphy, Qureshi, Sutton, O'Keefe, 2000).

Cases of temporally-graded retrograde amnesia are occasionally reported among human subjects with extensive medial temporal lobe damage. The typical symptom is a pattern of memory loss that affects recently formed memories, while leaving very remote memories (memories formed prior to the trauma) intact. Studies assessing pre-morbid memory loss for socially acquired information in rats have found similar temporal gradients associated with recall. The common finding is an impairment in performance when lesions to the hippocampal formation occur within 2 days of the learning phase. However, normal recall emerges if similar lesions are made approximately 2 to 5 or more days following the learning phase (Winocur, 2001).

The finding of temporally-graded retrograde amnesia suggests the existence of a critical window of hippocampal involvement following learning during which time the integrity of the hippocampus is essential for the viability of a memory. However, once a memory has survived this critical stage, it appears to no longer be reliant on the hippocampus for its expression.

1.6 General Working Hypotheses

The general purpose of Experiment 1A was to test the hypothesis that by better approximating the natural conditions under which STFP would occur in the wild, social learning in the laboratory would be facilitated. As such, Experiment 1A sought to emulate the naturalistic approach adopted by the Valsecchi group (1996), within a

laboratory setting, with rats as subjects instead of mice and with an important modification. In the Valsecchi study, observer mice, once exposed to demonstrator mice, were tested for socially transmitted food preferences in the continued presence of demonstrators along with other observers. Consequently, it is difficult to ascertain whether the tendency for the group to prefer the diet consumed by the demonstrator mice is a result of social transmission or due to some other combination of processes. For example, it is possible that demonstrator rats preferentially fed from food bowls containing the target diet (a diet more familiar to them then the alternative, unknown diet) and observers simply trailed demonstrators to the food site. In contrast to the Valsecchi (1996) study, and in an effort to gain more control over the test phase, Demonstrator rats from Experiment 1A were removed from the experimental situation following a fixed period of Demonstrator/Observer interaction and Observers were tested for food preference acquisition in isolation. The main prediction of Experiment 1 was that 'groups' of observer rats, interacting simultaneously, would readily acquire a food preference from a single; freely moving demonstrator rat pre-fed a distinctly flavored food.

Subjects used in the preponderance of STFP studies are the product of impoverished rearing conditions. In spite of this practice, rats do acquire food preferences and STFP is clearly a social phenomena. In contrast to common convention, subjects in Experiment 1A had at least 10 weeks of environmental enrichment from post weaning to young adulthood, prior to the start of testing. This regimen involved daily, scheduled access to large, multi level enriched environments during which time rats were exposed to other rats (a minimum of ten per cohort), diverse substrates (ranging from wood, to

bark, to sand, stone etc) and foraging experience (nuts, seeds, lard). To assess the effects of this important variable on food preference acquisition, subjects in Experiment 1B were reared according to standard housing protocol and were at no time exposed to any form of enriched housing. These rats provided a basis for assessing the interaction between enrichment and learning protocol on the acquisition of a food preference. It was hypothesized that rats reared under impoverished conditions and tested under conventional protocol would acquire a food preference from a conspecific, however, as a result of their impoverished social and experiential background, would be less likely to acquire as robust a preference from demonstrator rats as test matched rats in Experiment 1A.

In Experiment 2, Observer rats received sham surgery or hippocampal lesions and were tested under group-learning protocol. It was predicted that, if under group learning procedures, performance is dependent on the same neural processes as learning under the conventional approach; a similar pattern of results should be obtained. Therefore, it was hypothesized that hippocampal-lesion rats interacting in groups would readily acquire a food preference from a single, demonstrator rat, evident during the test phase, 10 min following learning.

EXPERIMENT 1A

STFP is conventionally studied by feeding a demonstrator rat a distinctly flavored food and then allowing it to interact with a single observer rat in a small, barren enclosure. Social learning is said to have occurred if the Observer subsequently consumes more of the target diet smelled on the breath of the Demonstrator than a second equally

palatable alternative. Wild rats are social, central place foragers that feed at a distance from the burrow and return to it once feeding is complete. A rat returning to the colony at the end of a foraging bout would have the opportunity to interact with not one, but multiple colony mates, simultaneously. If STFP is an important factor in guiding the food choices of feral rats, then, under test conditions that better match the natural form of this phenomenon, learning should be enhanced. As such, Experiment 1A was designed to test the hypothesis that multiple Observers interacting with a single Demonstrator within large complex environments would readily acquire a food preference following exposure to a recently fed conspecific. Furthermore, it was hypothesized that the robustness of social learning would be enhanced under group-learning versus conventional-learning protocol.

METHOD

Subjects

A total of 189 male, Long-Evans rats obtained from Charles River, Quebec (St Constant) served as subjects in the following series of experiments. Rats were received post weaning as 21-day-old pups, housed in pairs upon arrival in standard laboratory shoebox cages (18" x 9.4" x 8") and kept under a 12:12 light/dark cycle (light onset at 8:00pm). All rats were fed a basic laboratory rodent diet (name of diet) on a restricted-feeding schedule such that food availability was limited to a single, 1 hr feeding session a day. Experimentation for all rats began between the ages of 10 to 12 weeks (~ 70 days). All rats were experimentally naïve at the time of testing.

Environmental Enrichment

Beginning at the age of 28 days, and for the following 10 weeks, rats were placed into large, multi-level enriched environments, in groups of 10 to 15 rats. Enrichment sessions occurred exclusively during the dark phase of the rat's light cycle and spanned approximately 5 to 8 hr/day.

The enriched environments were large (58" x 25" x 57") multi-level free standing steel structures enclosed on three sides by wire mesh and on one side by clear Plexiglas. Enriched environments were made up of five separate levels, freely accessible to rats via passageways located at either end. Different kinds of substrates were used as bedding on the floor of each level including cedar bark, rocks, sand and wood shavings. During an enrichment session, rats were provided with the opportunity to forage for various foodstuffs including nuts, seeds, peanuts and rat chow.

Rats remained in fixed and familiar groups throughout the duration of the enrichment regimen. Top loaders (clear plastic shoebox cages), located on the uppermost level of the environments provided a stable entry and exit point for session start and end. Following a sessions end, rats were always returned to the colony for feeding.

Diets

Two distinctively flavored diets were prepared by mixing lard (Tenderflake, Loblaws, Quebec) with either 1% by weight powdered cinnamon (cinnamon diet) or 3% by weight powdered chocolate (chocolate diet). During testing, each of two diets were presented to subjects by means of two separate food cups affixed to metal hangers placed adjacent to one another at the ends of the test chambers. The positioning of the particular

diets during the test phase was counterbalanced to avoid the potentially confounding influence of a side bias. The same two test diets were used in all subsequent experiments.

Procedure

Habituation: conventional-learning. On the day prior to the start of testing, daily access to environmental enrichment was discontinued for subjects in the conventional-learning condition.

The purpose of the habituation phase was to familiarize rats with the procedural, material and contextual elements that would be present during the learning and test phases of the experiment. Over the course of three consecutive days, subjects were transported from their home cages to testing rooms and placed into separate shoebox cages (18" x 9.4" x 8") where they remained undisturbed for a period of 30 min. Shoebox test-cages were lined with thin cardboard sheets and contained two hanging food cups each containing small portions of unflavored lard. At the end of each habituation session, rats were returned to their home cages in the colony room where they remained until the following day. Despite the availability of lard during habituation, these sessions did not replace regular feeding, which occurred several hours post-habituation in the same manner as previously described. In preparation for the learning phase of testing, on the third day of habituation, Demonstrator rats were habituated to eating either unflavored lard, chocolate or cinnamon diet depending on group assignment. Pre-fed Demonstrator rats were separated from their Observer pairs at this stage of testing. Although Demonstrator and Observer pairs were habituated in the same manner and at the same

time of day, sessions occurred in separate rooms so as to avoid Observer rat exposure to experimental odors during the pre-feeding session.

Habituation: group-learning. Methodologically, habituation in the group-learning and conventional-learning conditions differed in only one respect. Rather than a complete cessation of the enrichment cycle prior to the start of experimentation, subjects in the group-learning condition were given continued daily access to the environments throughout habituation and during the learning phase of testing. Habituation spanned three consecutive days during which time Observer and Demonstrator rats adhered to the same daily enrichment regimen as during pre-experimentation. However, at the end of each enrichment session, rather than being returned to the colony room, subjects were transported to the same testing rooms as used in the conventional design for the final stage of habituation. In preparation for the learning phase, Demonstrator rats were habituated to eating one of three diets depending on group assignment in a separate room (unflavored lard, chocolate diet, or cinnamon diet).

Learning phase: conventional-learning. So as to minimize the likelihood of aggressive behavior between subjects during the learning phase, Demonstrator-Observer pairs were formed out of existing cage mates. These roles were randomly assigned prior to the habituation phase and remained unchanged throughout the three phases of experimentation. The learning phase began on the 4^{th} day following the last day of habituation. In preparation for the interaction session between Observers and Demonstrators, Demonstrator rats were allotted a minimum of 30 min to consume at least 1 gram of diet. Feeding times were extended to a maximum of $1^{1/2}$ hr to make allowances for Demonstrator rats refusing to eat during the first 30 min of the session. Each

Demonstrator was exposed to one of three flavored foods (unflavored lard, cinnamon diet or chocolate diet). Following feeding the experimental diet to Demonstrators, Demonstrator and Observer pairs were reunited for the interaction phase (shoebox cages) and left to interact freely for a period of 30 min. At the end of the 30 min interaction phase, Demonstrator rats were removed from the test chambers and returned to the colony room to be housed singly. All interactions were video recorded. Figure 1 depicts the learning phase for rats tested under conventional-learning protocol.

Learning phase: group-learning. Figure 2 depicts the enriched environments used for the multiple-observer–to-single-demonstrator interaction during the learning phase for rats tested under group-learning protocol. The learning phase began on the 4^{th} day following the last day of habituation. In preparation for the interaction session between Observers and Demonstrators, Demonstrator rats were offered either unflavored lard, chocolate diet, or cinnamon flavored diet and allotted a minimum of 30 min to consume at least 1 gram of diet. Feeding times were extended to a maximum of $1^{1/2}$ hr to make allowances for Demonstrator rats refusing to eat during the first 30 min of the session (Demonstrator rats were pulled from the 'enrichment' regimen on this day and only reunited with Observer rats during the interaction portion of the learning phase). Observers spent the conventional 5 hr period in enrichment prior to the interaction phase. At the end of the Demonstrator pre-feeding session, each Demonstrator rat was introduced into one of three environments, where it remained among multiple and familiar Observer rats for a period of no more than 30 min. All sessions were videotaped.

Test phase. Following the learning phase, subjects from both the group-learning and conventional-learning conditions were given either a 10 min or 24 hr retention

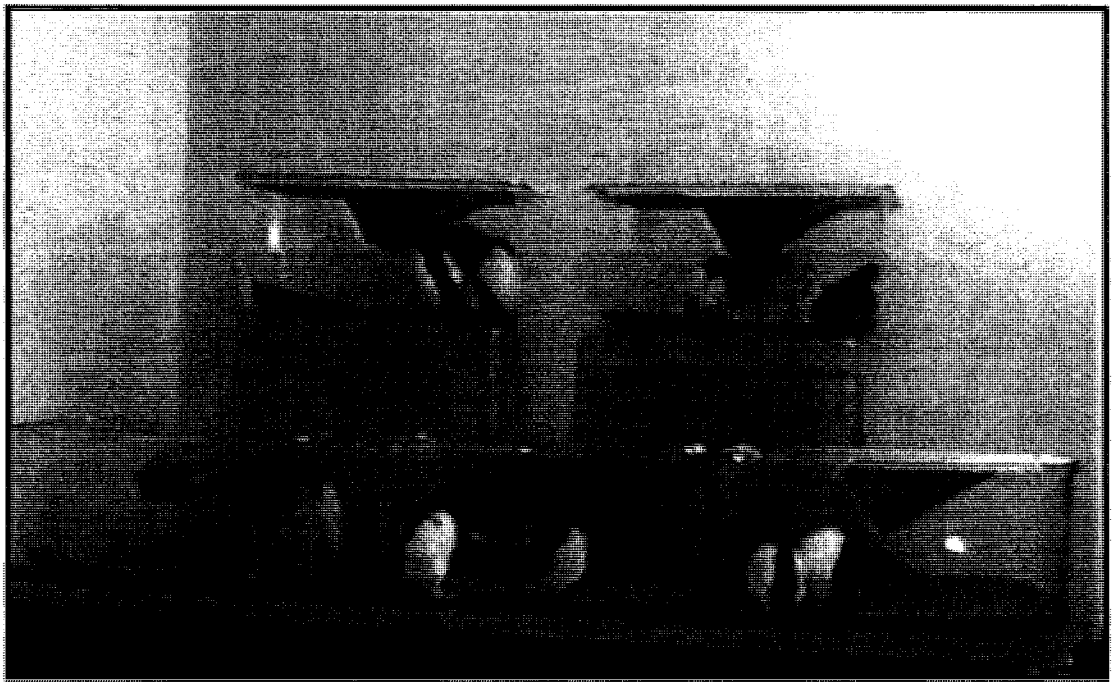


Figure 1. Shoebox cages used for the learning and test phases of the conventional-learning protocol, as well as the test phase of the group-learning protocol.

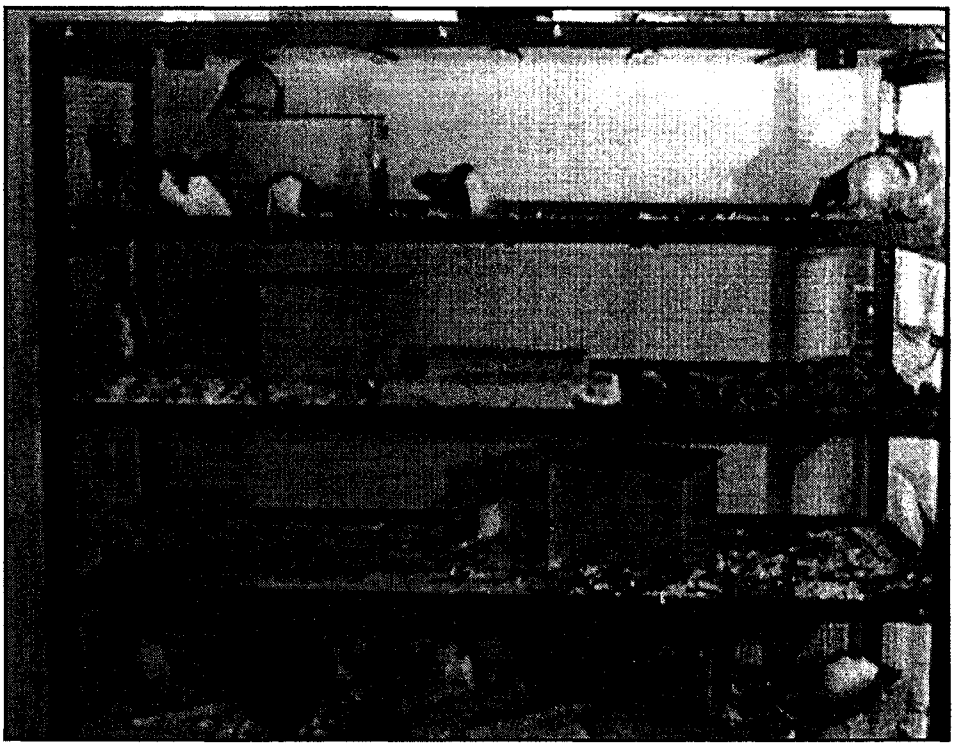


Figure 2. Enriched environments used for rearing rats in Experiments 1A and 2, and the learning phase of the group-learning condition.

interval prior to the test phase. During the 30 min test phase, Observer rats were offered two weighed hanging food cups – one contained cinnamon diet and the other contained chocolate diet. Each Observer was tested in a separate shoebox cage. At session end, Observer rats were returned to the colony room and reunited with Demonstrator pairs. Food jars were then removed and weighed so as to determine the amount of chocolate and cinnamon diet consumed by each rat.

Data analysis

Scoring. The time that Observers spent in investigation of Demonstrator rats during the learning phase was determined with the use of a stopwatch. To meet criterion, bouts of interaction between Observer/Demonstrator pairs were recorded only in instances of Observer rat investigation of the anterior portion of Demonstrator rats (instances of ano-genital investigation or investigation of a rats flanks were excluded). Additionally, Observer rats were required to be within 2 centimeters of the Demonstrator and oriented towards the Demonstrator's snout. So as to facilitate Observer/Demonstrator rat identification during the learning phase, Demonstrator rats were identified by markings placed on their flanks with a non-toxic black marker.

The scoring and marking criterion used in Experiment 1A was the same for all subsequent experiments.

Statistical Analysis

The results of Experiment 1 were analyzed simultaneously in 1, three-factor between subjects analysis of variance with Learning Condition (group-learning procedure

versus conventional-learning procedure), Demonstrator ('control'- Demonstrator fed unflavored lard, 'chocolate' - Demonstrator fed chocolate-flavored lard and 'cinnamon' - Demonstrator fed cinnamon-flavored lard) and Interval Length (10 min or 24 hr) serving as fixed factors. Due to known problems with the constrained nature of proportionalized data and the use of parametric statistics, an arcsin transformation was performed on the proportion of cinnamon consumed. The correlation between the transformed data and the original data was found to be statistically significant ($r(227) = .85, p < .05$). Based on this high level of correlation, all future analyses were performed on the original data set.

Proportions used in the ensuing analyses were computed by dividing each Observers total intake of cinnamon by each Observer's combined intake of cinnamon and chocolate during the test phase.

$$\text{Proportion of cinnamon consumed} = \frac{\text{grams of cinnamon consumed}}{\text{grams of (cinnamon + chocolate diets) consumed}}$$

Observer rats that consumed less than 1 gram of food during the preference tests were excluded from the analysis.

RESULTS

Consumption data

Figures 3 and 4 show the mean proportion of cinnamon consumed by Observer rats for both the group-learning and conventional-learning conditions, expressed as a function of Interval Length and Demonstrator.

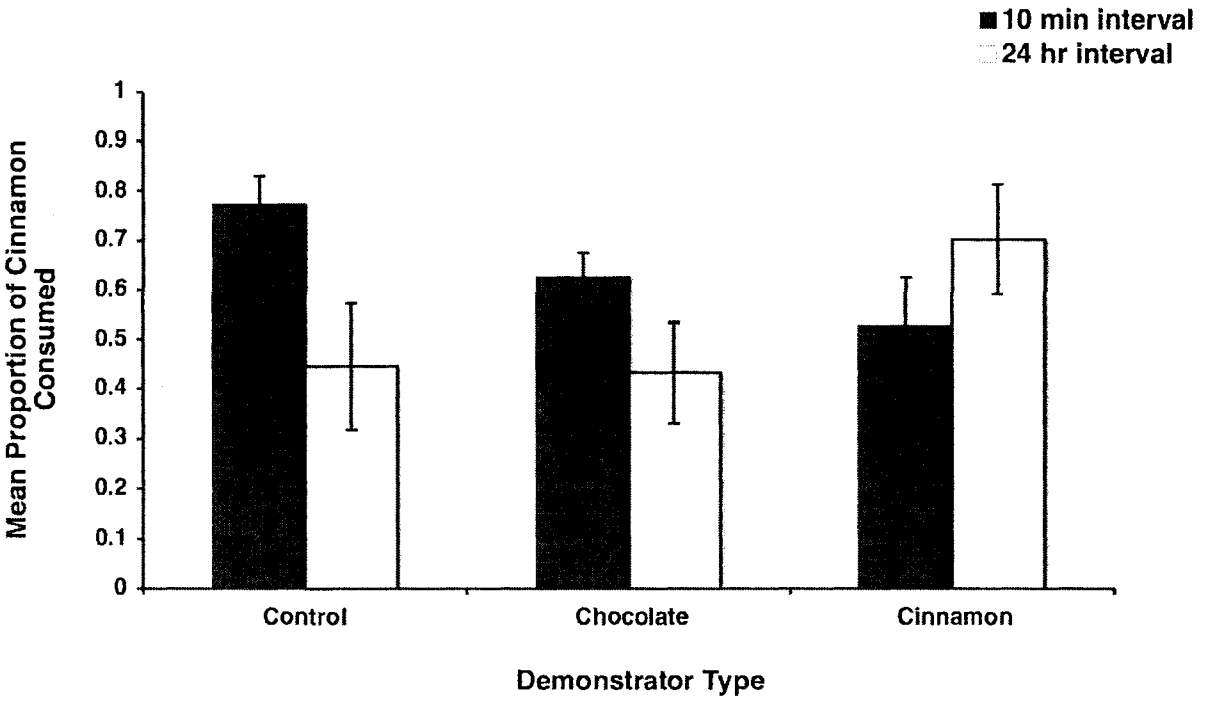


Figure 3. The mean proportion of cinnamon consumed by Observer rats during the preference test following interaction with a Cinnamon, Chocolate or Control Demonstrator rat, tested under conventional-learning protocol at either 10 min or 24 hr post learning. Error bars represent standard errors of means.

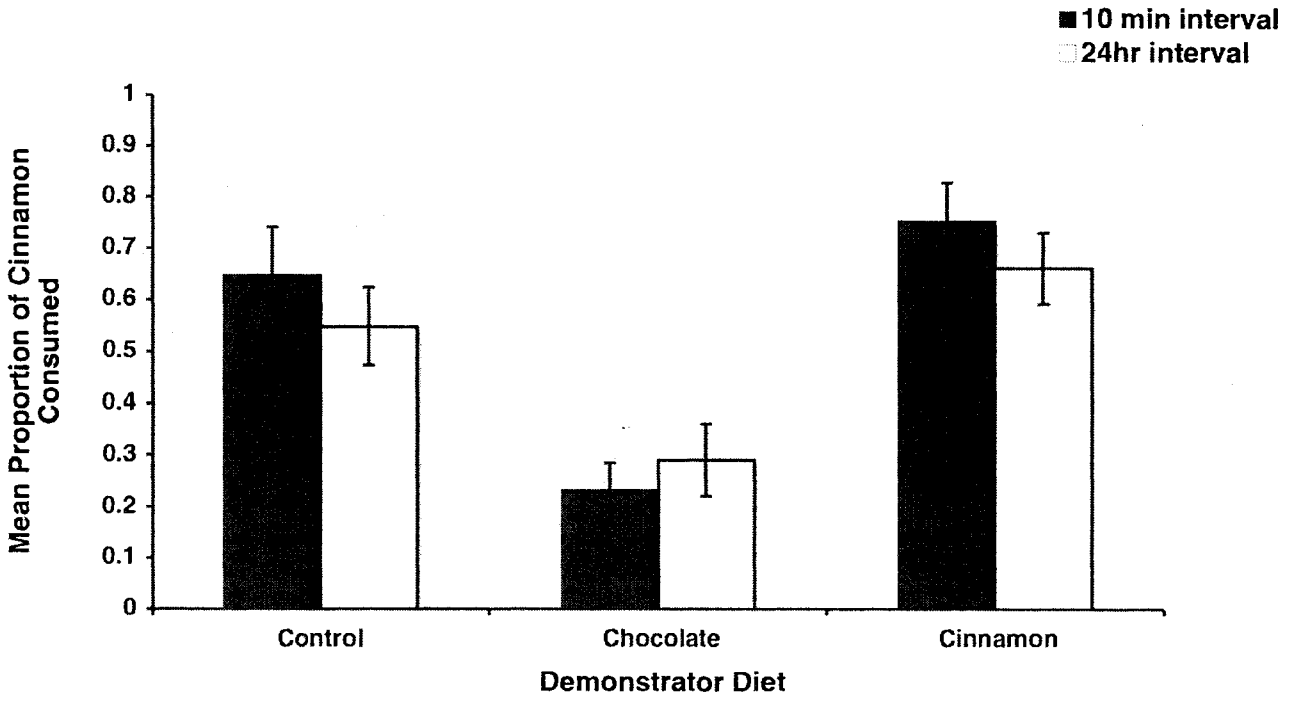


Figure 4. The mean proportion of cinnamon consumed by Observers during the preference test, following interaction with a Cinnamon, Chocolate or Control Demonstrator rat, tested under group-learning protocol at either 10 min or 24 hr post learning. Error bars represent standard errors of means.

A 3 X 2 X 2 between subjects ANOVA performed on the proportion of cinnamon consumed as a function of Learning Condition, Demonstrator and Interval Length, revealed a significant main effect of Demonstrator ($F(2, 164) = 12.85, p < .05, \eta^2 = .135$), as well as a significant Learning Condition X Demonstrator interaction ($F(2, 164) = 5.61, p < .05, \eta^2 = .064$) and a significant Interval X Learning Condition X Demonstrator interaction ($F(2, 164) = .05, p < .05, \eta^2 = .036$). The analysis further revealed non significant main effects of Interval Length and Learning Condition ($F(1, 164) = 2.82\ p > .05$, $F(1, 164) = 1.76\ p > .05$; respectively); and a non significant Interval X Learning Condition and Interval X Demonstrator interaction ($F(1, 164) = .55, p > .05$, $F(2, 164) = 2.276, p > .05$; respectively). To further assess the three-way interaction, 2 two-factor between subjects ANOVAs were performed.

Group-learning. Analysis of the proportion of cinnamon diet consumed in the group-learning condition revealed a significant main effect of Demonstrator ($F(2, 87) = 19.57, p < .05, \eta^2 = .31$); a non significant main effect of Interval Length ($F(1, 87) = .520, p > .05$); and a non significant Interval Length X Demonstrator interaction ($F(2, 87) = .708, p > .05$). Post-hoc analyses of the main effect of Demonstrator revealed that Observers consumed significantly less cinnamon when exposed to a Chocolate Demonstrator relative to Observers exposed to a Control Demonstrator (mean difference: 0.3266, $p < .05$; control > chocolate) and Observers exposed to a Cinnamon Demonstrator consumed significantly more cinnamon that Observers exposed to a Chocolate Demonstrator (mean difference: -0.4385, $p < .05$; cinnamon > chocolate).

A series of one-sample *t*-tests to compare the mean proportion of cinnamon diet consumed as a function of Demonstrator diet to chance levels (test value 0.5) were

performed. Since earlier analyses revealed a non significant interaction between Interval Length and Demonstrator, the following tests were performed on data collapsed across time intervals. The results of these analyses revealed that control rats performed at chance, preferring neither chocolate nor cinnamon diets ($t(29) = 1.55, p > .05$). Observer rats exposed to a Chocolate Demonstrator performed significantly different from chance ($t(29) = -5.171, p < .05$), with a proportion of total cinnamon intake of .29. Conversely, Observer rats whose Demonstrator rat had consumed cinnamon diet performed significantly different from chance ($t(32) = 3.995, p < .05$), with a proportion of total cinnamon intake of .70.

Conventional-learning. Analysis of the proportion of cinnamon diet consumed in the conventional-learning condition revealed a non significant main effect of Interval Length ($F(2, 77) = 2.524, p > .05$); a non significant main effect of Demonstrator ($F(2, 77) = 0.716, p > .05$) and a significant interaction between Interval Length and Demonstrator ($F(2, 77) = 3.681, p < .05, \eta^2 = .087$). To assess the interaction between Interval Length and Demonstrator, 2 one-way ANOVAs were performed at each level of interval. At 10 min following the learning phase, a significant effect of Demonstrator was found ($F(2, 52) = .046, p < .05$), however, post-hoc Games-Howell tests failed to find any significant differences between groups. The Games-Howell test is used when sample sizes vary between groups and the assumptions of heterogeneity and normality cannot be assumed.

A one-way ANOVA performed on data from the 24 hr condition revealed a non significant effect of Demonstrator ($F(2, 25) = 1.69, p > .05$).

Total food consumed. A supplementary measure of consumption, total amount of

food consumed, was computed by summing the amount of chocolate and cinnamon flavored lard eaten during the test phase by Observer rats. Figures 5 and 6 present data for the average amount of food consumed (in grams) by Observer rats in the group-learning procedure and the conventional-learning procedure as a function of Interval Length and Demonstrator.

The results of a three-way between subjects ANOVA performed on the total amount of food consumed as a function of Learning Condition, Demonstrator and Interval Length revealed non significant main effects of Interval Length ($F(1, 164) = 2.175, p > .05$); Learning Condition ($F(1, 164) = 1.04, p > .05$) and Demonstrator ($F(2, 164) = 2.81, p > .05$). Interactions between Interval Length and Demonstrator ($F(2, 164) = 2.16, p > .05$) Demonstrator and Learning Condition ($F(2, 164) = .736, p > .05$) and Interval Length and Learning Condition ($F(1, 164) = 1.54, p > .05$) failed to achieve statistical significance. Overall, Observer rats consumed an average of 6.1 grams of food ($SD = 4.19$) during their preference tests regardless of Learning Condition, Interval Length and Demonstrator.

Proportion of Demonstrator-Matched diet consumed. So as to facilitate comparison between the performance of Observers tested under group-learning and conventional learning protocol, a second analysis was performed on the proportion of Demonstrator-Matched diet consumed by Observer rats (the same method of data comparison was used by Winocur and Moscovitch (1999)). The overall proportion of Demonstrator-Matched diet consumed for each learning condition was computed according to the following formula:

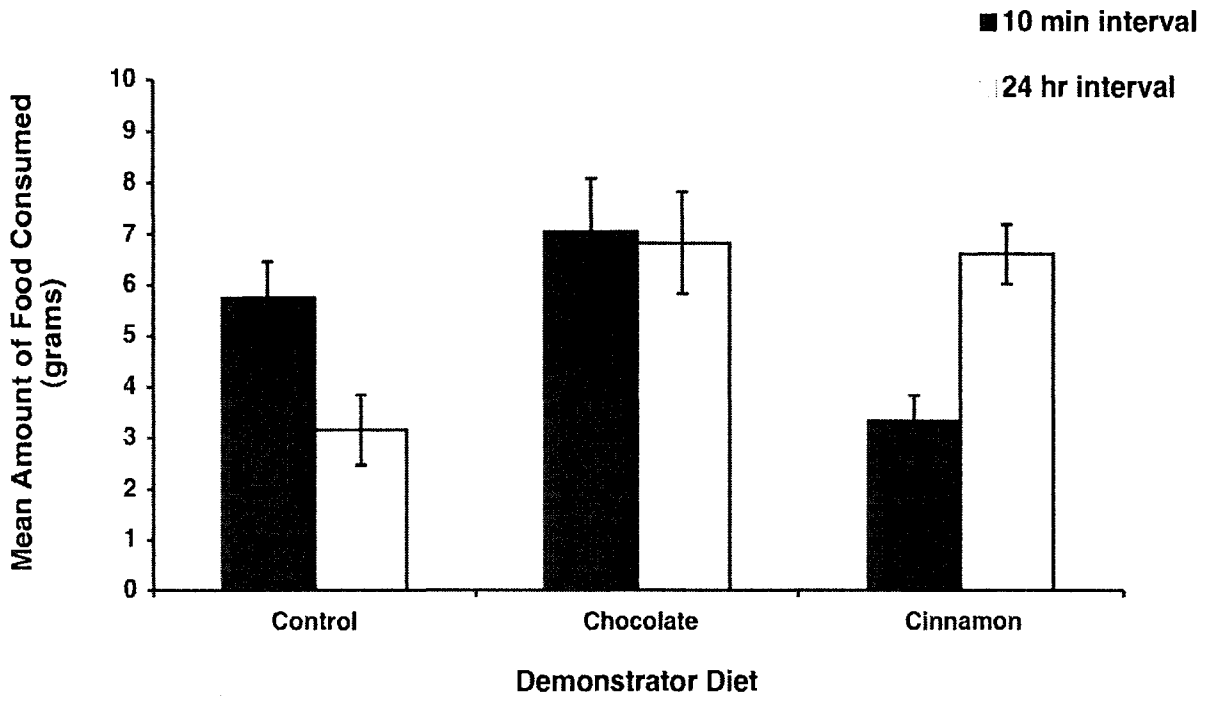


Figure 5. The mean amount of chocolate and cinnamon consumed by Observers during the preference test, following interaction with a Cinnamon, Chocolate or Control Demonstrator rat, tested under conventional-learning protocol at either 10 min or 24 hr post learning. Error bars represent standard errors of means.

$$\frac{\text{proportion of cinnamon consumed } \textit{(following exposure to a Cinnamon Demonstrator)} + \text{proportion of chocolate consumed } \textit{(following exposure to a Chocolate Demonstrator)}}{\text{total number of subjects}}$$

An independent samples *t*-test revealed a significant difference in the amount of Demonstrator-Matched diet consumed as a function of Learning Condition ($F(1, 116) = 17.61, p < .05, \eta^2 = .13$). Subjects in the conventional-learning condition consumed on average less Demonstrator-Matched diet ($M = .49$, $SD = .31$) than subjects from the group-learning condition ($M = .72$, $SD = .27$). The results are depicted in Figure 7.

Performance of Controls

Figure 8 depicts the proportion of cinnamon consumed as a function of Learning Condition for control animals (Observers whose Demonstrators consumed unflavored lard), collapsed across Interval Length. An independent samples *t*-test revealed a similar preference for cinnamon among control animals in the conventional-learning condition ($M = .69$, $SD = .31$) and the group-learning condition ($M = 0.59$, $SD = 0.32$) ($t(56) = 1.19$) $p > .05$). Control Observers tested under conventional and group-learning conditions did not differ in their intake of cinnamon during the preference test.

Interaction data

The amount of time (Interaction Time) Observer rats spent in snout-to-snout contact with Demonstrator rats was tabulated for all conditions in which this was possible. In certain cases, interactions were either not recorded or could not be seen because of the positioning of rats. Refer to Figure 10 for a graphical depiction of missing

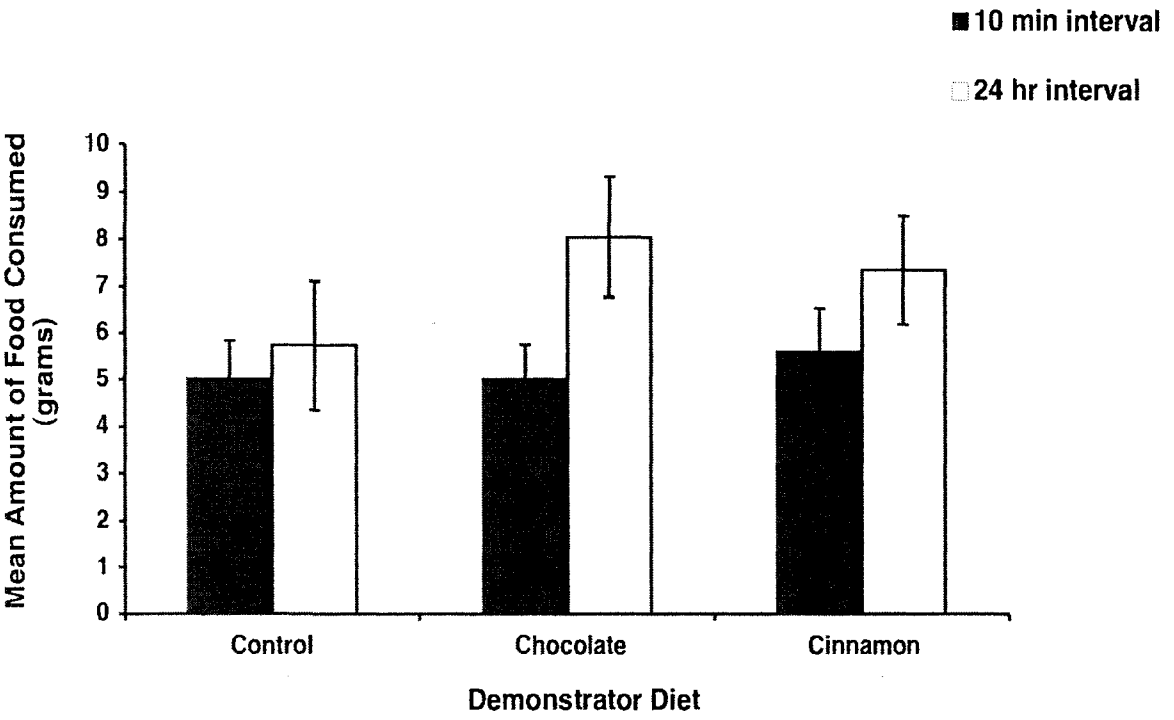


Figure 6. The mean amount of chocolate and cinnamon consumed by Observers during the preference test, following interaction with a Cinnamon, Chocolate or Control Demonstrator rat, tested under group-learning protocol at either 10 min or 24 hr post learning. Error bars represent standard errors of means.

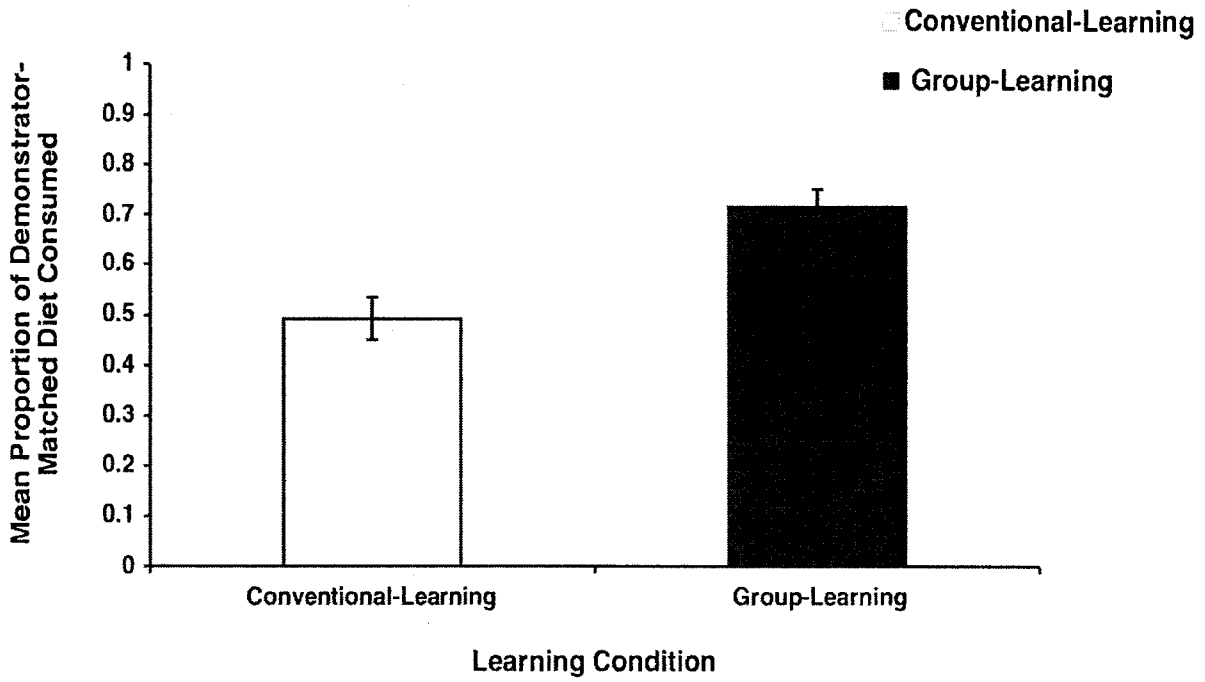


Figure 7. The mean proportion of Demonstrator-Matched diet consumed by Observers during the preference test following exposure to a Chocolate or Cinnamon Demonstrator and tested under conventional or group-learning conditions. Error bars represent standard errors of means.

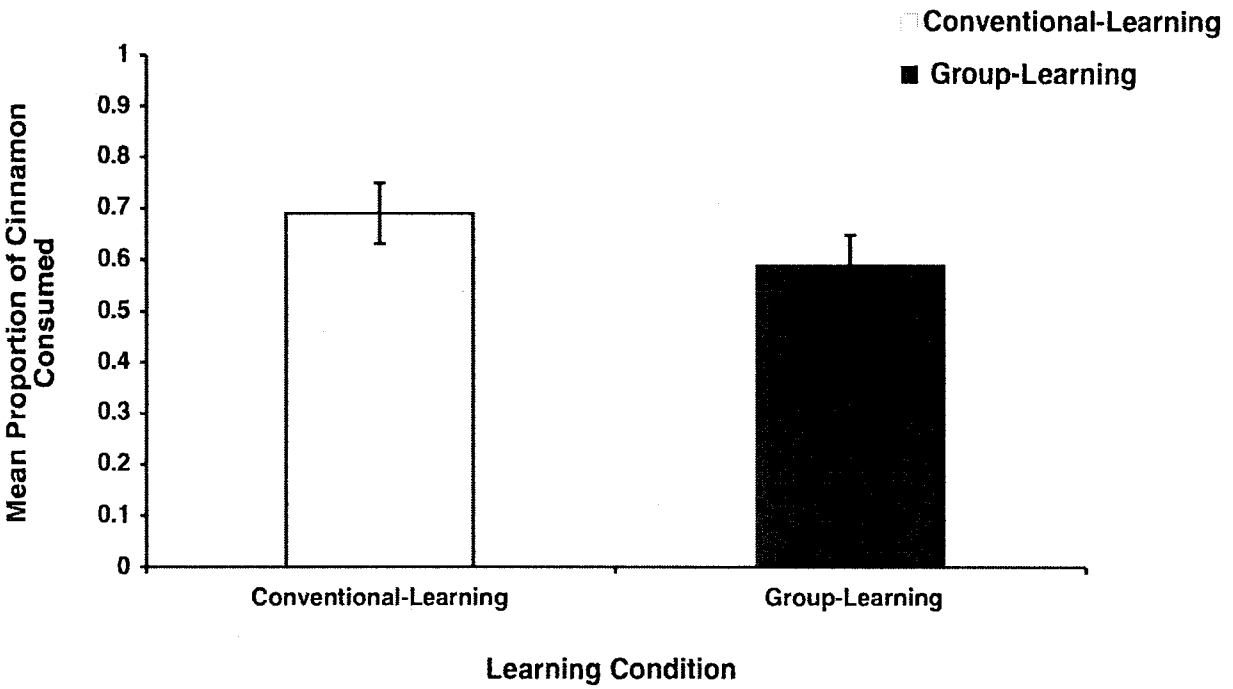


Figure 8. The mean proportion of cinnamon consumed by Control Observers during the preference test of conventional-learning or group-learning conditions. Data points are collapsed across Interval Length. Error bars represent standard errors of means.

data.

To determine whether the mean amount of time Observer rats spent in investigation of Demonstrator rats differed with respect to Demonstrator and Learning Condition; a two-factor between subjects analysis of variance with Interaction Time as the dependent variable was performed. Due to a lack of test-matched interaction data for the 24 hr interval, conventional-learning procedure, only interaction data from the 10 min interval were examined.

Results of the two-way analysis of variance revealed a significant main effect of Learning Condition ($F(1, 71) = 18.24, p < .05, \eta^2 = .204$); and a non significant main effect of Demonstrator ($F(2, 71) = .207, p > .05$) and Demonstrator X Learning Condition interaction ($F(2, 71) = 0.316, p > .05$).

A visual summary of the final result is presented in Figure 9. Data points represent interaction scores collapsed across Demonstrator for data obtained from the test phase at 10 min following the learning phase. Observer rats in the group-learning condition spent an average of 26.13 seconds (SD = 22.38) in snout-to-snout contact with Demonstrator rats while Observer rats in the conventional-learning procedure spent an average of 170.20 seconds (SD =148.25). Figure 10 represents all available interaction data as a function of Interval Length, Learning Condition and Demonstrator.

Figure 11 depicts the fluctuations in interaction over time (30 min session divided into six, 5 min bins) as a function of Experimental Group (Control Demonstrator versus Chocolate and Cinnamon Demonstrator) and Learning Condition (group-learning versus conventional-learning). A 2 X 2 X 6 mixed factorial ANOVA with Time as the within subjects factor, revealed a significant main effect of Learning Condition ($F(1, 141) =$

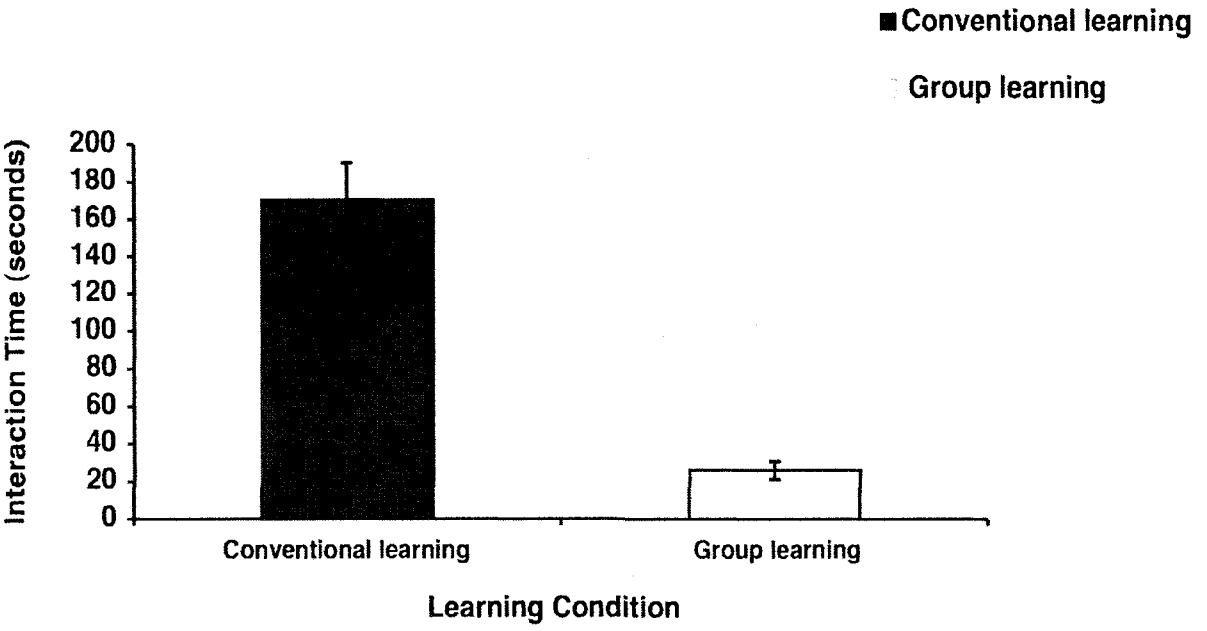


Figure 9. The mean amount of time Observers spent in snout-to-snout contact with Demonstrator rats during the learning phase of the conventional or group-learning conditions. Error bars represent standard errors of means.

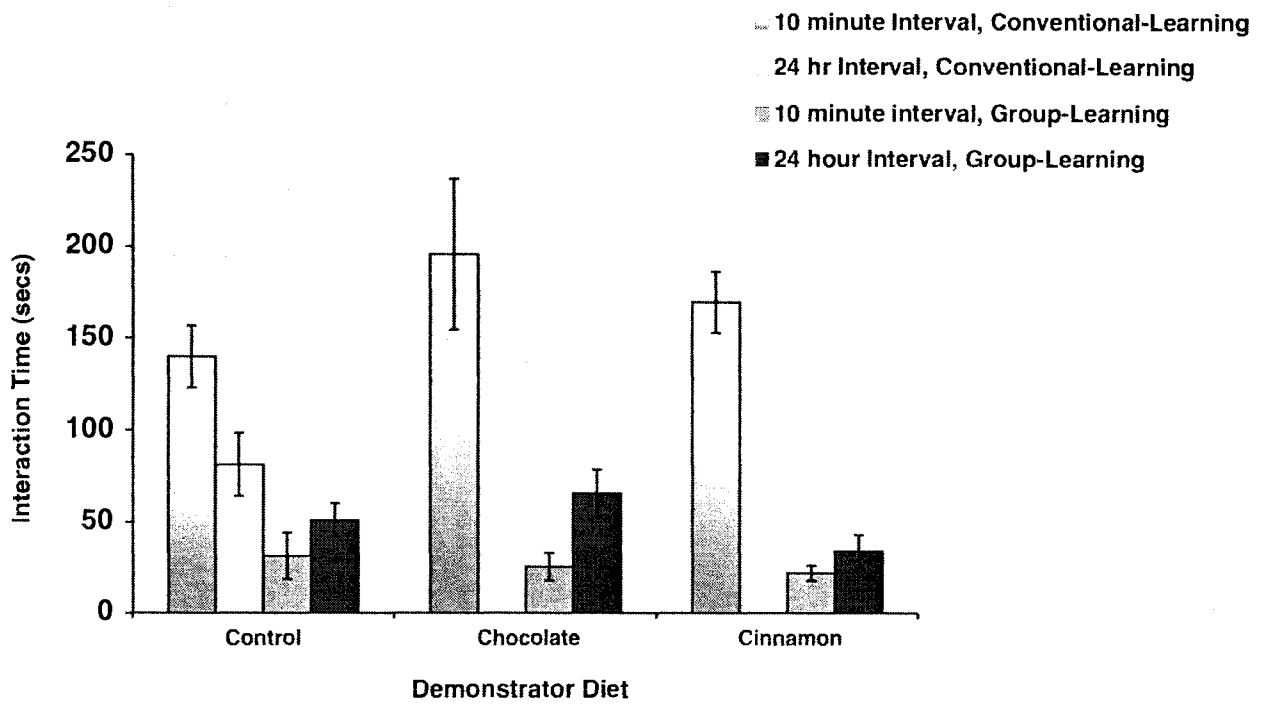


Figure 10. The mean amount of time Observers tested under group or conventional – learning protocol (following a 10 min or 24 hr retention interval) spent in snout-to-snout contact with Control, Chocolate or Cinnamon fed Demonstrators during 30 minutes of free interaction. Error bars represent standard errors of means.

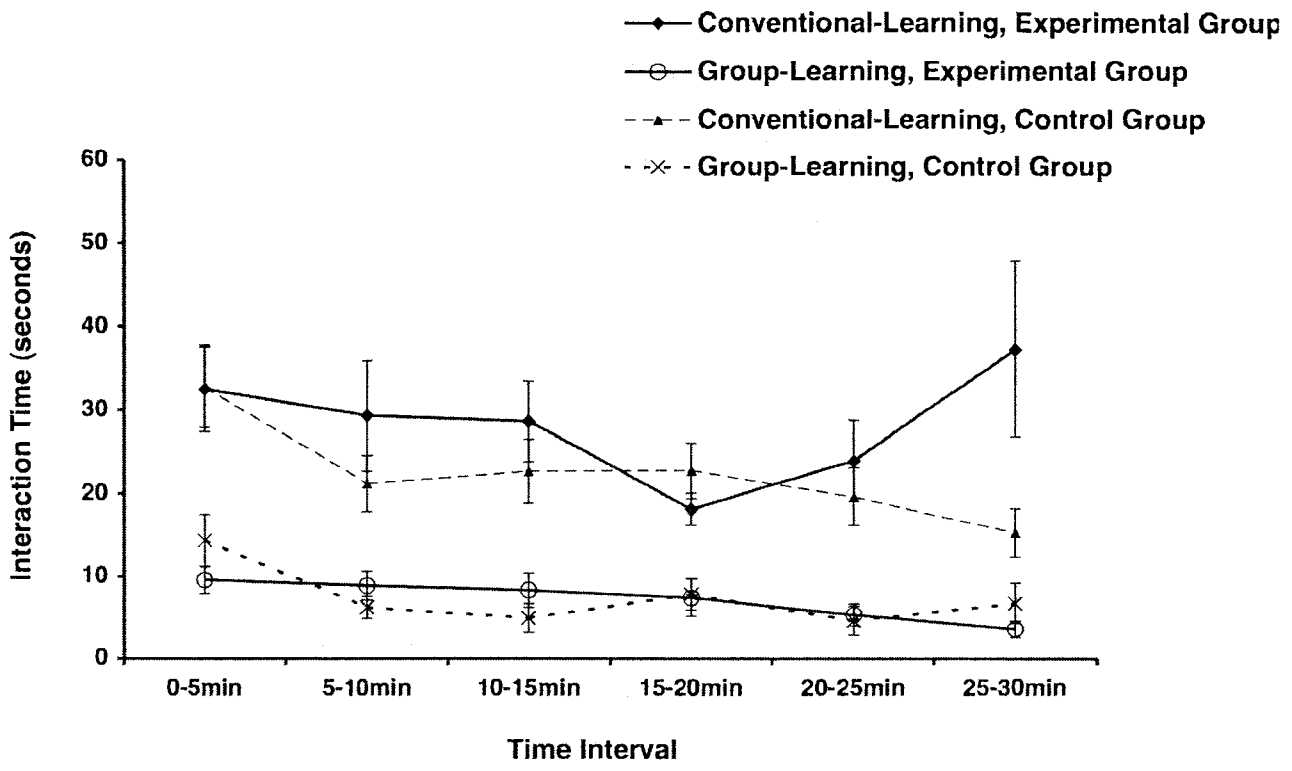


Figure 11. The mean amount of time Observers spent in snout-to-snout contact with Control, or Chocolate and Cinnamon (Experimental Group) Demonstrator rats during the 30 min learning phase. Interaction times are divided into 5 min intervals. Data points represent interaction times as a function of conventional or group-learning protocol. Error bars represent standard errors of means.

30.08, $p < .05$, $\eta^2 = .18$) and a non significant main effect of Experimental Group ($F(1, 141) = 2.25$, $p > .05$). The interaction between Learning Condition and Experimental Group was non significant ($F(1, 141) = .342$, $p > .05$).

Demonstrator consumption

A two-way between subjects ANOVA was carried out in an effort to determine if the amount of diet consumed by Demonstrator rats prior to the interaction phase differed with respect to diet consumed and Learning Condition.

The results of the analysis revealed a main effect of Demonstrator ($F(2, 85) = 30.60$, $p < .05$, $\eta^2 = .42$) and a main effect of Learning Condition ($F(1, 85) = 4.612$, $p < .05$). A non significant interaction was found between Demonstrator and Learning Condition ($F(2, 85) = 0.615$, $p > .05$). Games-Howell post-hoc analyses were performed to assess the main effect of Demonstrator collapsed across Learning Condition. The results of the analysis revealed that Control Demonstrators ate significantly more diet (unflavored lard) than either Chocolate Demonstrators ($p < .05$) or Cinnamon Demonstrators ($p < .05$). Chocolate Demonstrators and Cinnamon Demonstrators did not differ with respect to intake ($p > .05$).

Demonstrator rats consumed an average of 3.32 grams of chocolate diet ($SD = 1.93$), 3.88 grams of cinnamon diet ($SD = 2.2$) and 8.6 grams of unflavored lard ($SD = 3.39$). Demonstrators in the conventional-learning condition consumed an average of 5.15 grams of diet ($SD = 3.71$) while Demonstrators from the group-learning condition consumed an average of 3.87 grams of diet ($SD = 2.14$). These data are depicted in Figure 12.

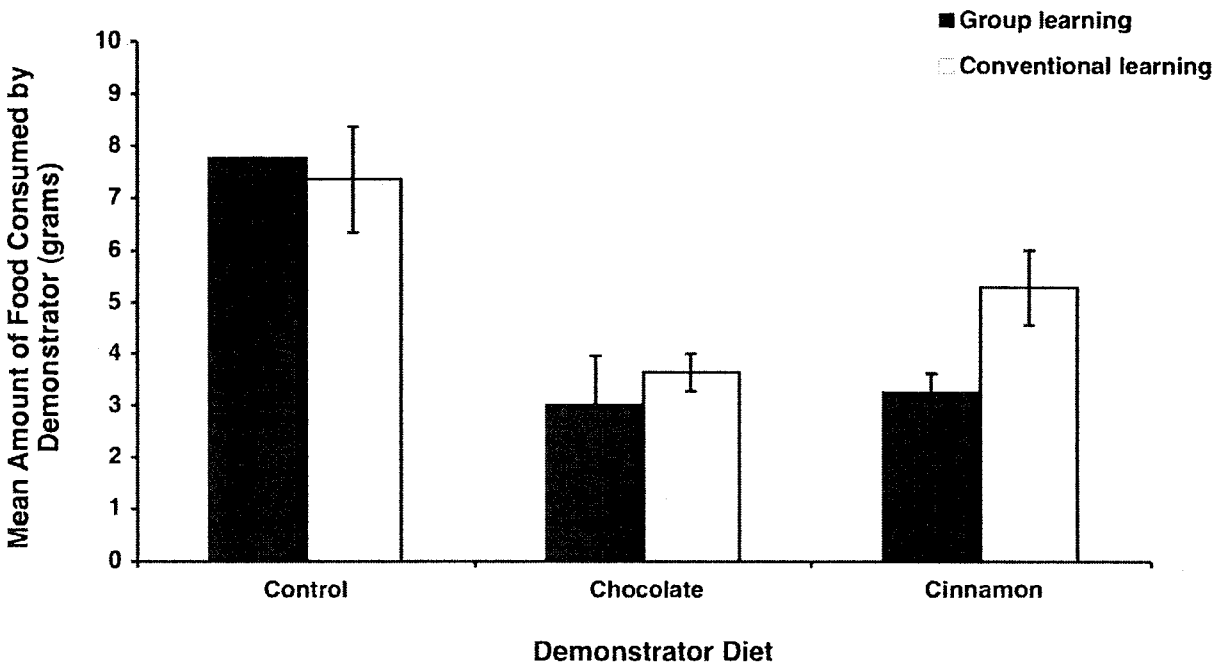


Figure 12. The mean amount of unflavored lard, chocolate or cinnamon consumed by Demonstrator rats prior to exposure to Observers from either the conventional or group-learning condition. Error bars represent standard errors of means.

Correlational Analyses

Correlational analyses were performed to assess the relationship between Interaction Time (the amount of time spent in interaction with Control, Chocolate or Cinnamon Demonstrators) and the proportion of Demonstrator-Matched diet consumed by Observers during the test phase. Each learning condition was assessed separately. The results of the analysis at each level of Learning Condition, revealed a non significant Pearson correlation between variables for both the group-learning procedure ($r(48) = -.063, p > .05$) and the conventional-learning procedure ($r(18) = -0.079, p > .05$).

For each learning condition, the relationship between Interaction Time and the quantity of diet consumed by Demonstrator rats prior to the interaction phase was also assessed. There was a non significant correlation for both the group-learning procedure ($r(30) = -.079, p > .05$) and the conventional procedure ($r(18) = -.116, p > .05$).

DISCUSSION

Rats interacting in large groups with a single Demonstrator rat readily acquired a food preference. Observer rats that were exposed to a Chocolate Demonstrator consumed proportionately more chocolate than cinnamon in the preference test. Similarly, Observer rats that interacted with a Cinnamon Demonstrator rat consumed proportionately more cinnamon than chocolate diet. Conversely, Observers exposed to a Demonstrator that ate the lard base of those diets did not prefer either, and consumed equal proportions of both chocolate and cinnamon diets during the preference test. Food preferences acquired by subjects in the group-learning condition were equally robust at 10 min and 24 hr following the learning phase.

These data indicate that under group-learning conditions, multiple rats can acquire a food preference from a single Demonstrator rat.

In contrast, subjects tested under conventional-learning protocol performed less consistently than subjects in the group-learning condition. For example, the magnitude of the acquired preference was greater in the group-learning condition than in the conventional-learning condition. Furthermore, rats tested under conventional procedures did not show an effect of Demonstrator at either retention interval.

Several factors may account for the failure of rats tested under conventional protocol to display as robust a food preference as Observers tested under group protocol.

For example, Galef has provided evidence suggesting that the greater the proportion of Demonstrators that have consumed a particular diet present during the interaction phase, the greater the preference of their Observers for that diet (Galef et al., 1990). It is conceivable that this effect is a result of a general increase in the salience of the target diet as a result of greater exposure to its odor. Variability in the amount of diet consumed by Demonstrator rats and therefore the strength of olfactory cues emanating from the breath of Demonstrators during the interaction phase may explain the failure for rats tested under conventional protocol to acquire/display a food preference. However, two lines of evidence mitigate against this explanation. Demonstrators in the group-learning condition consumed, on average, less diet than Demonstrators in the conventional-learning condition, yet their Observers still acquired a food preference. Furthermore, the amount of diet consumed by Demonstrator rats was not found to be predictive of the Observer's later food preferences in either the group or conventional-learning conditions.

Additionally, one might predict that less time spent learning about a flavored food might translate into less of a preference for that particular food. Interestingly, the amount of time animals spent in snout-to-snout contact with Demonstrator rats differed substantially between learning conditions, but not in the direction one might expect in light of the main finding. Observers interacted with Demonstrators for an average of 23 seconds in the group-learning condition and 138 seconds in the conventional-learning condition. In neither condition was amount of time spent in snout-to-snout contact with Demonstrator rats a good predictor of food preferences. Collectively, these findings suggest that the strength of flavor cues emanating from Demonstrators and time spent interacting with a Demonstrator cannot explain the differences in the magnitude or reliability of preferences acquired by observers in the two learning conditions.

EXPERIMENT 1B

In Experiment 1A, subjects tested under conventional-learning procedures failed to display a food preference following exposure to a Chocolate or a Cinnamon Demonstrator rat. This finding was somewhat unexpected considering rats from this condition were treated, from a procedural standpoint, in the same way as the prototypical subject tested under procedures devised by Galef and Wigmore (1983). However, differences in rearing conditions and the early experiences of rats from this cohort may account for the discrepant result. In the preponderance of STFP research, subjects are raised under standardized housing protocol, characterized by low stimulation levels and barren living conditions. In Experiment 1, subjects received exposure to environmental enrichment for several hours a day and for a period of at least 10 weeks. Experiment 1B

was carried out as a preliminary step at assessing the influence of environmental enrichment on the acquisition of a food preference under conventional-learning procedures. Animals in Experiment 1B were maintained under standard laboratory housing conditions (Wurbel, 2000), without access to the enriched environments used in Experiment 1A.

METHOD

Subjects

The subjects were 32, experimentally naïve, 10 week old, male, Long-Evans rats acquired from Charles River, Quebec (St Constant). All rats were maintained in pairs in standard laboratory housing and kept on a 12:12 hr light/dark cycle (light onset at 8pm). All rats were fed a basic laboratory rodent diet on a restricted feeding schedule as in the manner described for rats in Experiment 1A.

Procedure

Procedurally, subjects in Experiment 1B were treated identically to subjects in Experiment 1A tested at 10 min following the learning phase.

Pre-habituation. In preparation for testing, subjects from this cohort of rats were habituated to being 'handled'. These sessions occurred on a daily basis and continued until rats appeared at ease with the sights, sounds and general features that accompany the presence of a human experimenter.

Statistical Analysis

In the following series of statistical analyses, data from the impoverished rat conditions was compared to test-matched data from Experiment 1A (subjects tested under conventional procedures following a 10 min retention between the learning and test phase).

RESULTS

Error variance

A Levene's test assessing the equality of variance between groups revealed no significant differences in error variance between the impoverished and enriched conditions ($F(1, 43) = .012, p > .05$).

Consumption data

Performance of controls. With regard to cinnamon consumption during the test phase, Control Observers (Observers whose Demonstrators consumed unflavored lard) from the impoverished and enriched conditions did not differ significantly in their preference for cinnamon ($t(26) = 1.23, p > .05$) (Figure 13). In lieu of these findings, and so as to facilitate comparison between impoverished and enriched animals tested under conventional-learning procedures, the overall proportion of Demonstrator-Matched diet consumed was computed.

Proportion of Demonstrator-Matched diet consumed. An independent samples *t*-test assessing the proportion of demonstrator matched diet consumed as a function of Rearing Conditions revealed a significant overall effect of Rearing Condition ($t(43) = -$

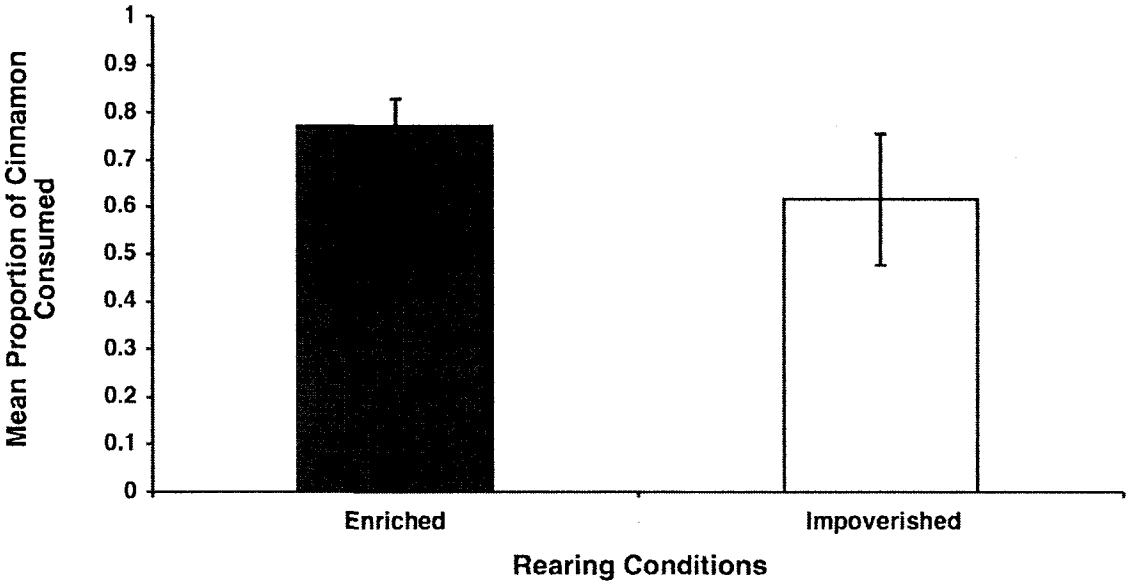


Figure 13. The mean proportion of cinnamon consumed by Control Observers during the preference test following exposure to a Control Demonstrator and reared under enriched or impoverished conditions. Error bars represent standard errors of means.

3.092, $p < .05$). Subjects from impoverished housing conditions ate significantly more Demonstrator-Matched diet ($M = 0.71$, $SD = 0.28$) than their enriched counterparts ($M = .42$, $SD = .26$). These findings are depicted in Figure 14.

A two way analysis of variance performed on the average amount of food consumed by Observer rats during the test phase as a function of Demonstrator and Rearng Condition revealed non significant main effects of Demonstrator (F (2, 67) = 1.623, p > .05) and Rearing Condition (F (1, 67) = 1.826, $p > .05$) and a non significant Demonstrator X Rearing Condition interaction (F(1, 67) = 1.003, $p > .05$). These data can be seen in Figure 15.

Interaction data

The mean amount of time subjects spent in interaction with Demonstrator rats as a function of Rearing Condition and Demonstrator was assessed with a two-way between subjects ANOVA. The results of the analysis revealed non significant main effects of Demonstrator and Rearing Condition (F(2, 67) = 1.286, $p > .05$, F(1, 67) = 0.213, $p > .05$) and a non significant Demonstrator X Rearing Condition interaction (F(2, 67) = 0.196, $p > .05$). This finding is depicted in Figure 16. Subjects from the impoverished condition spent an average of 146 ($SD = 70.73$) seconds with Demonstrator rats while subjects from the enriched condition spent an average of 170.2 seconds ($SD = 148.25$).

Figure 17 depicts the fluctuations in interaction over time (30 min session divided into six, 5 min bins) as a function of Experimental Group (Control Demonstrator versus Chocolate and Cinnamon Demonstrator) and Rearing Condition (Impoverished versus Enriched). A 2 X 2 X 6 mixed factorial ANOVA with Time as the within-subjects factor

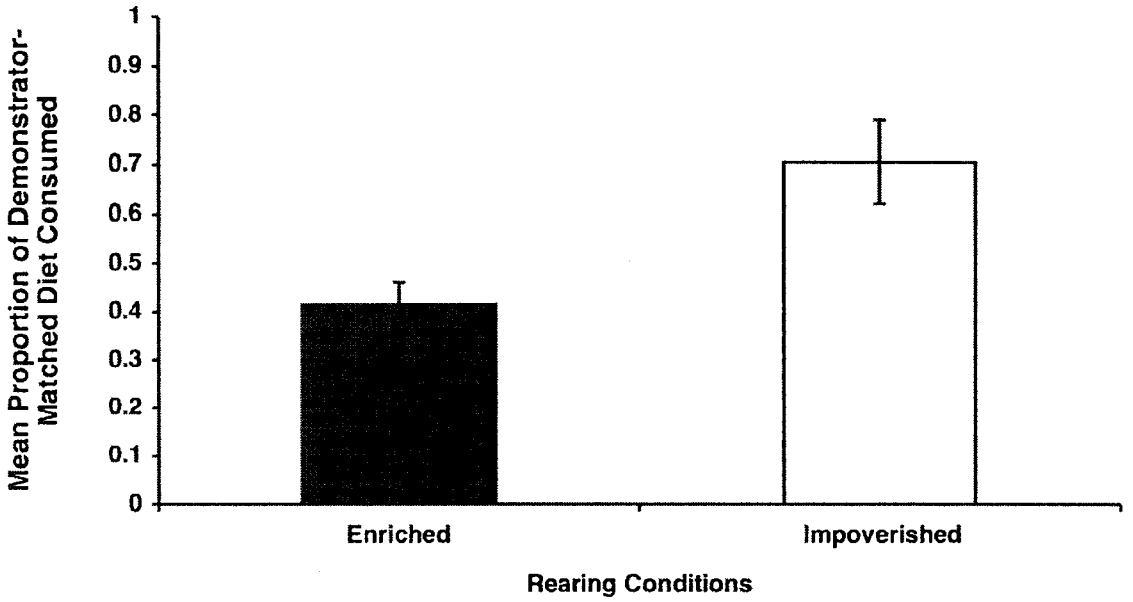


Figure 14. The mean proportion of Demonstrator-Matched diet consumed by Observer rats raised under enriched or impoverished conditions. Observers were tested under conventional protocol with a 10 min retention interval between the learning and test phase. Control group data are excluded. Error bars represent standard errors of means.

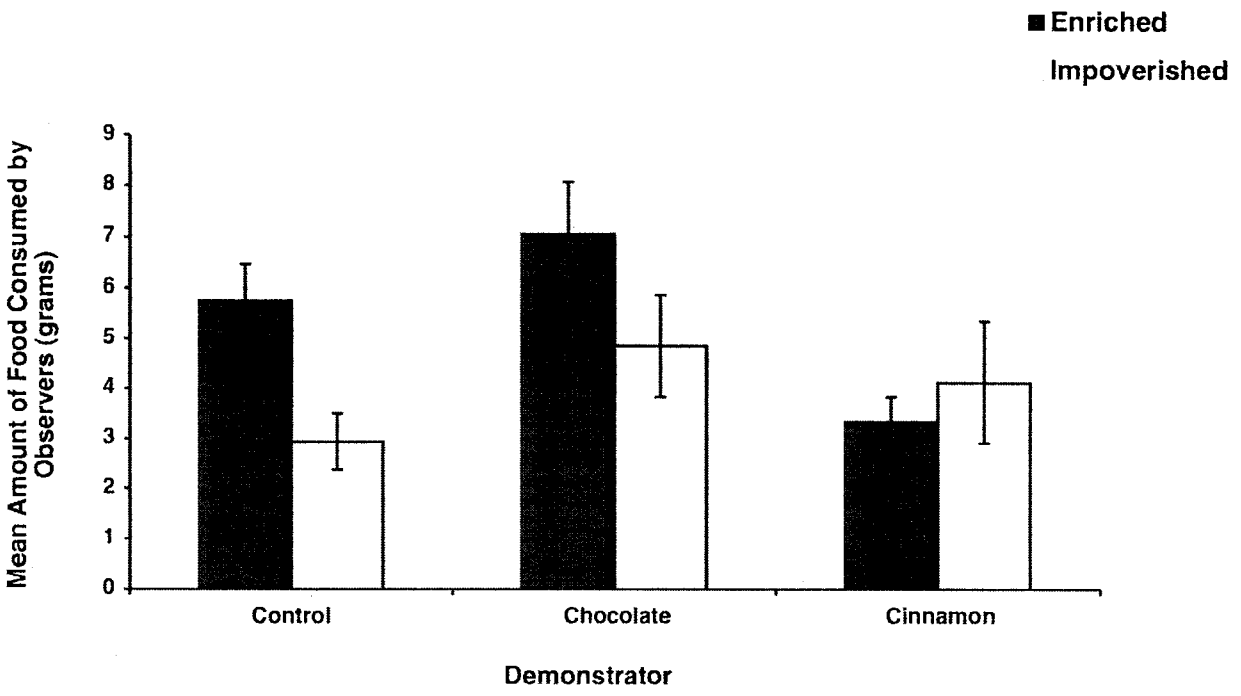


Figure 15. The mean amount of Chocolate or Cinnamon diet consumed by Observers tested under conventional-learning protocol, exposed to a Control, Chocolate or Cinnamon fed Demonstrator and reared under enriched or impoverished conditions. Error bars represent standard errors of means.

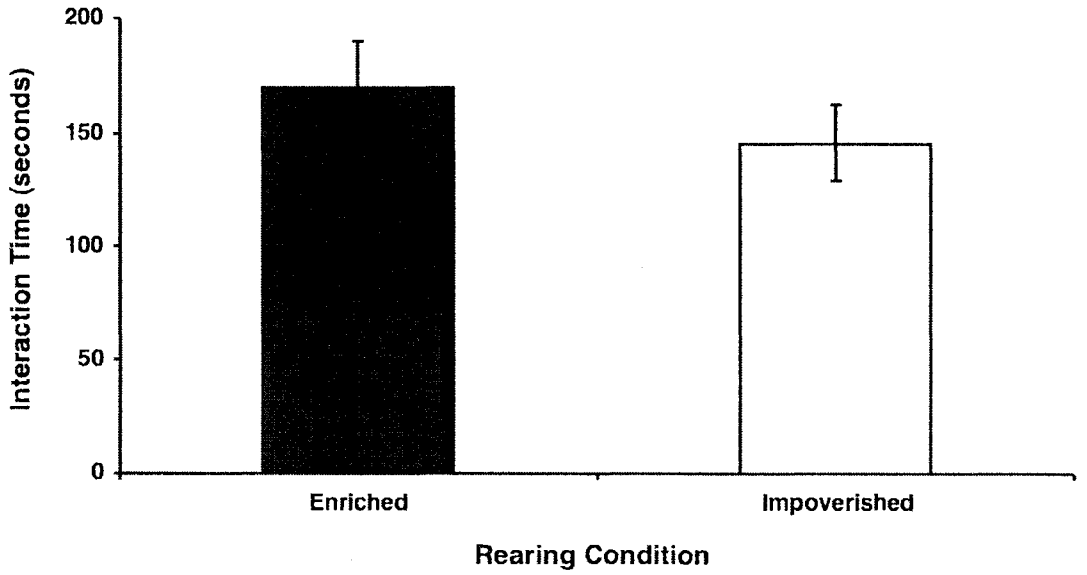


Figure 16. The mean amount of time Observers spent in snout-to-snout contact with Chocolate and Cinnamon fed Demonstrator rats as a function of enriched or impoverished rearing conditions. Observers were tested under conventional-learning protocol. Error bars represent standard errors of means.

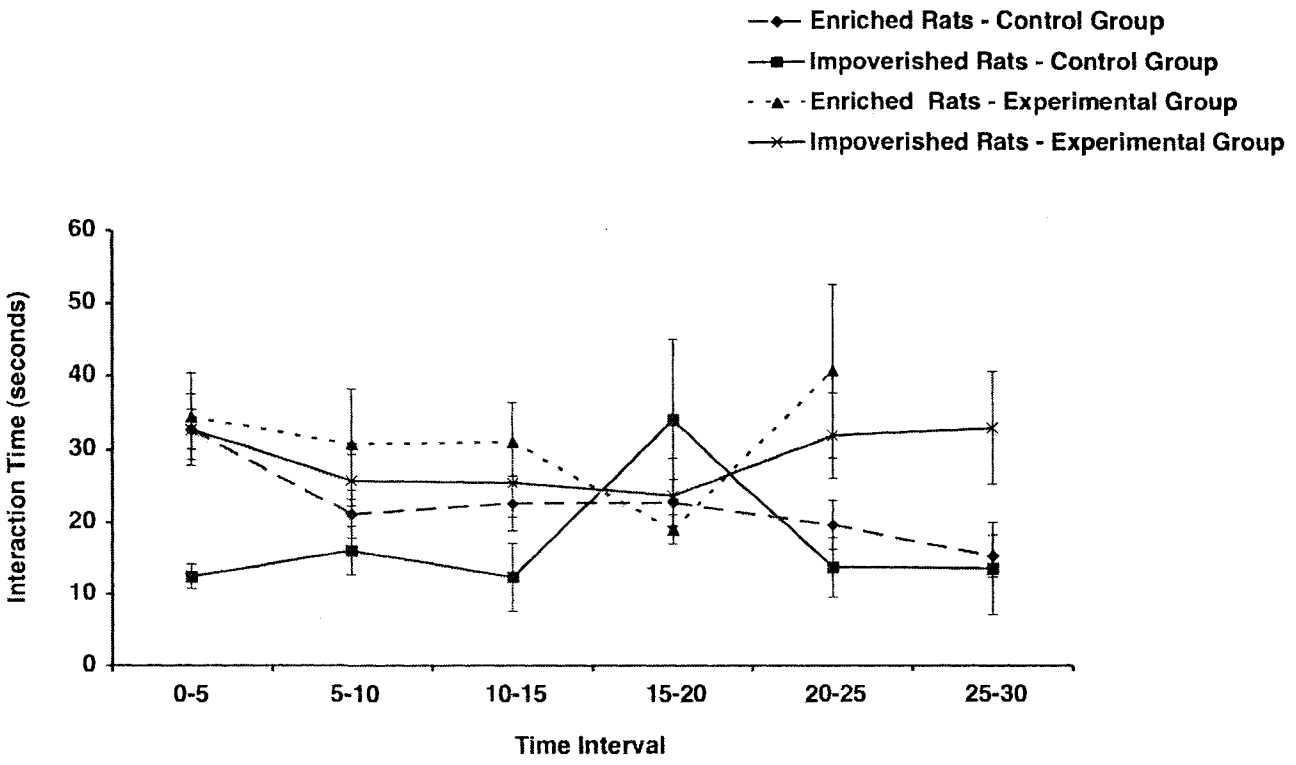


Figure 17. The mean amount of time Control, or Chocolate and Cinnamon Demonstrator rats spent in snout-to-snout contact with Observer rats during 30 minutes of interaction. Interaction times are divided into 5 min intervals. Data points represent interaction times as a function of rearing condition (enriched or impoverished). Error bars represent standard errors of means.

revealed non significant main effects of Experimental Group ($F(1, 80) = 3.428, p > .05$) and Rearing Condition ($F(1, 80) = .457, p > .05$) and a non significant interaction between Rearing Condition and Experimental Group ($F(1, 80) = .093, p > .05$).

Demonstrator consumption

The amount of diet consumed by Demonstrator rats prior to exposure to Observer rats as a function of Rearing Condition and Demonstrator was compared by means of 2-way between subjects ANOVA. The results revealed non significant main effects of Demonstrator ($F(2, 59) = 3.64, p > .05$) and Rearing Condition ($F(1, 59) = 1.71, p > .05$) and a significant interaction between Demonstrator and Rearing Condition ($F(2, 59) = 4.92, p < .05$). Demonstrator rats from the impoverished condition consumed an average of 4.26 grams of lard ($SD = 3.37$), 4.4 grams of chocolate flavored lard ($SD = 1.59$), and 5.71 grams of cinnamon flavored lard ($SD = 2.77$). Demonstrator rats from the enriched condition consumed on average 9.03 grams of unflavored lard ($SD = 3.37$), 3.62 grams of chocolate flavored lard ($SD = 2.42$) and 5.07 grams cinnamon flavored lard ($SD = 2.83$). These findings are depicted in Figure 18.

Correlational analyses

A correlational analysis between the amount of time Observers from the impoverished condition spent interacting with Demonstrator rats and the proportion of diet consumed during the test phase was non significant ($r(11) = .35, p > .05$).

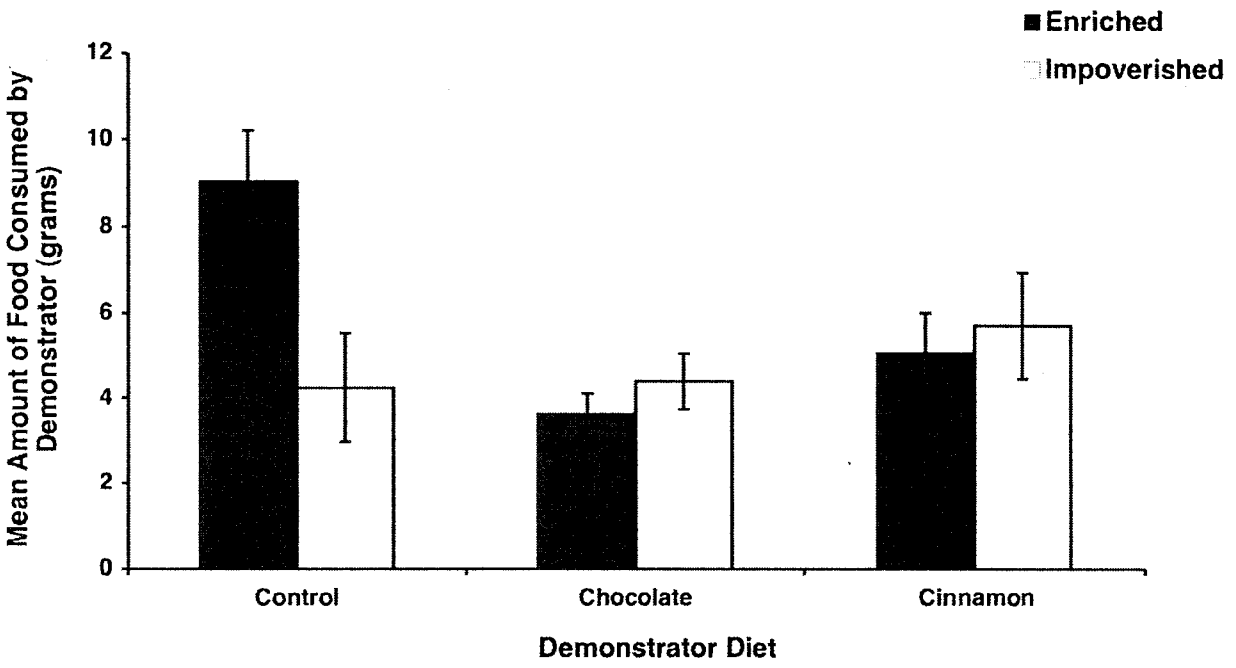


Figure 18. The mean amount of unflavored lard, chocolate or cinnamon diet consumed by Demonstrator rats exposed to Observers reared under impoverished or enriched rearing conditions. Observers were tested under conventional-learning protocol. Error bars represent standard errors of means.

DISCUSSION

The main finding of Experiment 1B was that subjects raised under standard housing conditions and tested under the conventional-learning protocol, were, on average, more likely to consume the foods encountered in association with Demonstrator rats than subjects from the enriched-rearing condition in Experiment 1A, tested under a similar learning protocol. The difference in performance between groups could not be accounted for by discrepancies in the amount of diet Demonstrator rats consumed prior to the interaction phase or by differences in the amount of time Observers spent in contact with Demonstrator rats. Interestingly, animals from the impoverished conditions acquired a preference that was much more similar in magnitude to that acquired by subjects raised under enriched conditions, tested under the new group-learning protocol than enriched rats tested under conventional–learning protocol (70% versus 76% versus 41%; respectively).

EXPERIMENT 2

Studies addressing the contribution of the hippocampal memory system to the acquisition and retention of a socially transmitted food preference converge on similar findings; the hippocampus is necessary for successful recall at long intervals following the learning phase (24 hr or greater), however, recall at short intervals appears to be hippocampus independent (Bunsey et al., 1995; Clark et al., 2002; Winocur, 2001). Procedurally, these studies employ testing protocol similar to those devised by Galef, whereby a single Observer interacts with a Demonstrator fed one of two distinctly scented diets (Galef & Wigmore, 2003). By contrast, in Experiment 2, performance of

rats with and without hippocampal damage was assessed under the group-protocol. It is predicted that rats with hippocampal lesions will acquire a food preference when the test and learning phase are separated by a short retention interval. This outcome is predicted based on the assumption that the same neural processes subserving the acquisition and retention of a food preference under conventional-learning protocol will be activated when learning occurs under group procedures.

METHOD

Subjects

The subjects were 20 male, Long-Evans rats obtained from Charles River, Quebec (St Constant). Rats were received post-weaning as 21-day-old pups, housed in pairs in standard laboratory shoebox cages and kept under a 12:12 light/dark cycle (light onset at 8:00pm). All rats were fed a basic laboratory Rodent Diet on a restricted feeding schedule as in the manner described for rats in Experiment 1.

Environmental enrichment

Beginning from the age of 28 days, rats received daily exposure to environmental enrichment. Environmental enrichment was terminated following 4 weeks of exposure in preparation for surgery.

Surgery

Rats either received hippocampal-lesions (n = 10) or sham-lesions (n = 10). Rats were given an injection of atropine sulfate approximately 30 min before anaesthetization

with isoflurane. All surgical coordinates were based on Paxinos and Watson's (1986) sterotaxic coordinates. A stereotaxic apparatus was used for all surgeries. HPC lesions were made using n-methyl-d-aspartic acid (3 mg dissolved in 0.051M phosphate buffered saline, PBS pH = 7.4; Sigma chem. Co., St. Louis, MO). The NMDA was infused over 5 sites bilaterally at a flow rate of 0.15 ul/min over a period of 2.5 min for a total injection volume of 0.4 ul of NMDA per site. Injections were made using a microinfusion pump (KD Scientific) and 10 ul Hamilton Syringes. The injection cannulae were 30 gauge needles through which the neurotoxin was infused using PE50 tubing connected to a Hamilton Syringe. To allow the neurotoxin to diffuse away from the cannulae, the cannulae were left in place for 2.5 min following the infusion before being removed. Sham animals underwent an incision and anesthesization with isoflurane, however, holes were not drilled and cannualae were not lowered into the brain.

Following surgery, all animals were treated with a topical antibiotic powder (Cicatrin) to the incision wound. Hippocampal-lesion rats received 0.2 ml of diazepam upon awakening in order to prevent seizure activity. Rats were allowed to recover for 14 days during which time they were given ad lib access to food.

Post-surgery. Following recovery, rats were returned to a fixed feeding schedule and were placed back on an enrichment schedule for a period of one week prior to testing.

Procedure

Hippocampal-lesion and sham-lesion animals were treated identically to subjects in Experiment 1A tested with a 10 min retention interval between the learning and test phase. However, only data for Observers exposed to Control and Cinnamon Demonstrators were analyzed.

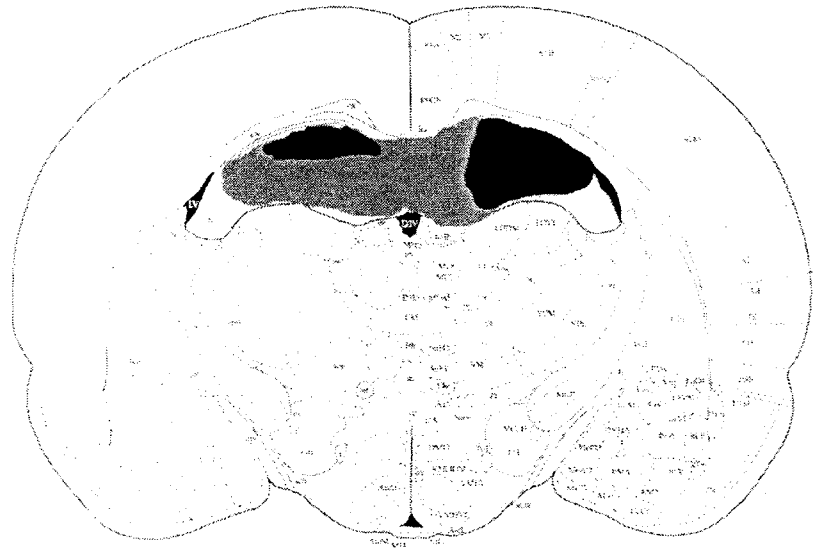
Histology

Following testing, rats received an overdose of sodium pentobarbital, i.p, and were perfused through the heart with 0.9% saline followed by 10% buffered formalin. Brains were extracted and transferred to a 30% sucrose-formalin solution for a period of 2 days in preparation for slicing. All brains were frozen sectioned at 30 μm, every 6^{th} section throughout the HPC was mounted on a glass microscope slide, and stained with cresyl-violet.

RESULTS

Histological Results

Figure 19 shows the location and extent of the largest and smallest of the hippocampal lesions. NMDA injections resulted in substantial cell loss in all principle subfields of the hippocampus and dentate gyrus. This loss was most pronounced in the dorsal hippocampus. There was some variability in damage to the ventral hippocampus and as well as in the extent of extra-hippocampal damage. In some cases, rats appeared to sustain more damage to one hemisphere.



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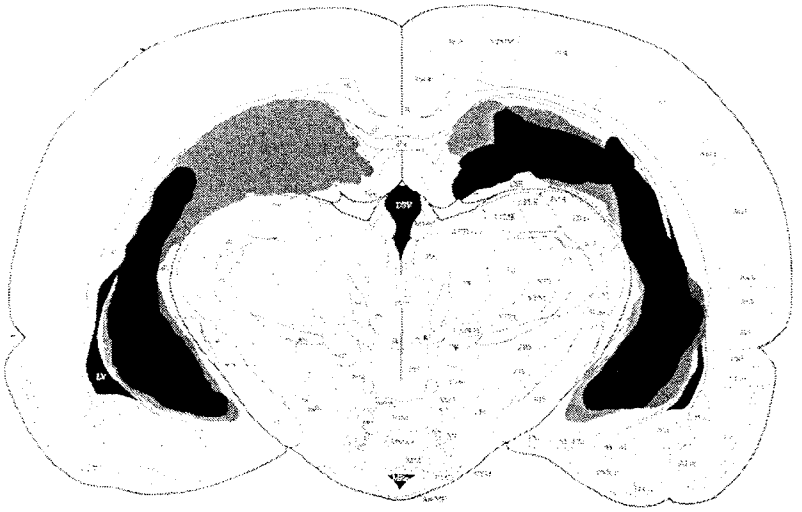

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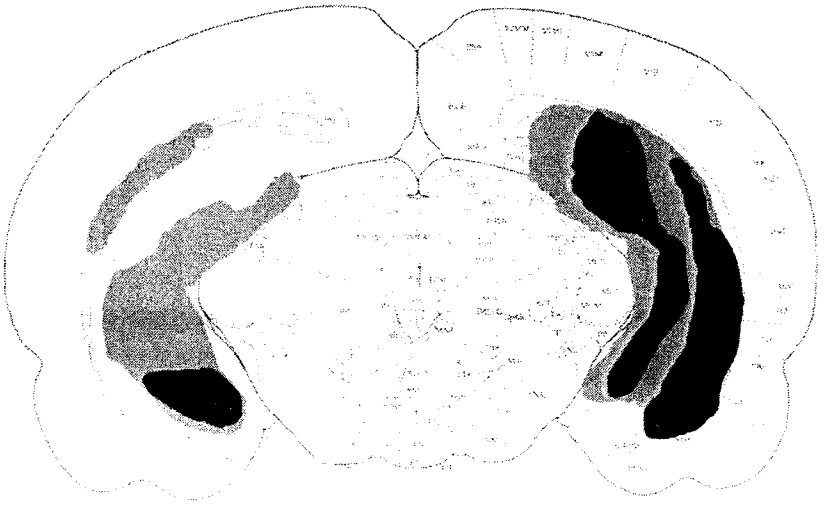

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Figure 19. A schematic representation of the coronal view of the largest and smallest HPC lesions. The largest HPC lesion is represented by the light shading and the smallest HPC lesion is represented by the dark shading. (Adapted from Paxinos and Watson, 1986).

Behavioral Results

Consumption data

Hippocampal-lesion, sham-lesion and no-surgery control rats (from a test-matched condition) served as levels for the factor 'Lesion' in the following analyses.

A two-way between-subjects ANOVA performed on the mean proportion of cinnamon consumed as a function of Demonstrator and Lesion revealed non significant main effects of Demonstrator ($F(1, 42) = 1.41, p > .05$), Lesion ($F(2, 42) = 1.72, p > .05$) and a non significant Lesion X Demonstrator interaction ($F(2, 42) = .01$, $p > .05$). Figure 20 shows these data.

A two-way ANOVA was performed to assess the total amount of food consumed as a function of Lesion and Demonstrator. The results revealed a non significant main effect of Lesion ($F(2, 42) = 1.697, p > .05$ and Demonstrator ($F(1, 42) = 2.978, p > .05$) and a non significant Demonstrator X Lesion interaction ($F(2, 42) = .091, p > .05$) (Figure 21).

Interaction data

A two-way ANOVA was performed to assess the average amount of time Observer rats spent interacting with Demonstrator rats as a function of Lesion and Demonstrator. The results of the analysis revealed a significant main effect of Lesion ($F(2, 29) = 6.396, p < 0.05, \eta^2 = .31$), a non significant main effect of Demonstrator ($F(1, 29) = .999, p > .05$) as well as a non significant Demonstrator X Lesion interaction ($F(2, 29) = .107, p > .05$). Post hoc Games-Howell tests were performed to assess the main effect of Lesion. The analysis indicated that the amount of time Observers spent interacting with Demonstrators did not differ between hippocampal-lesion rats and sham-

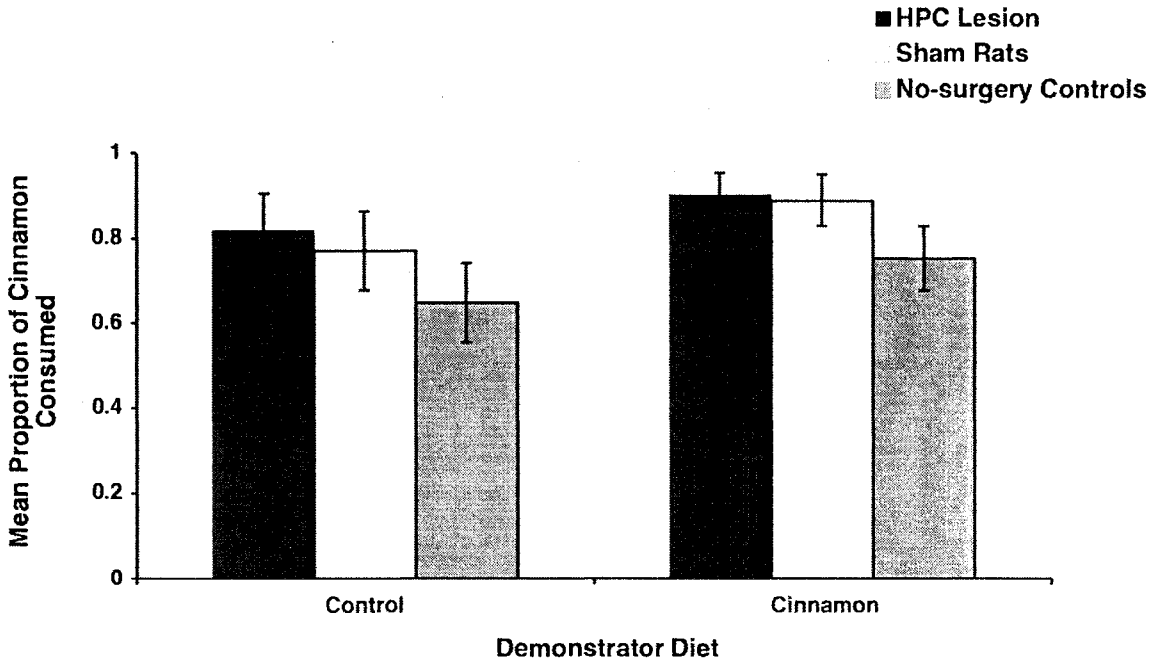

Figure 20. The mean proportion of cinnamon consumed by hippocampal-lesion, sham-lesion or no-surgery Observers during the preference test, exposed to either a Cinnamon or Control Demonstrator and tested under group-learning protocol at 10 minutes following the learning phase. Error bars represent standard errors of means.

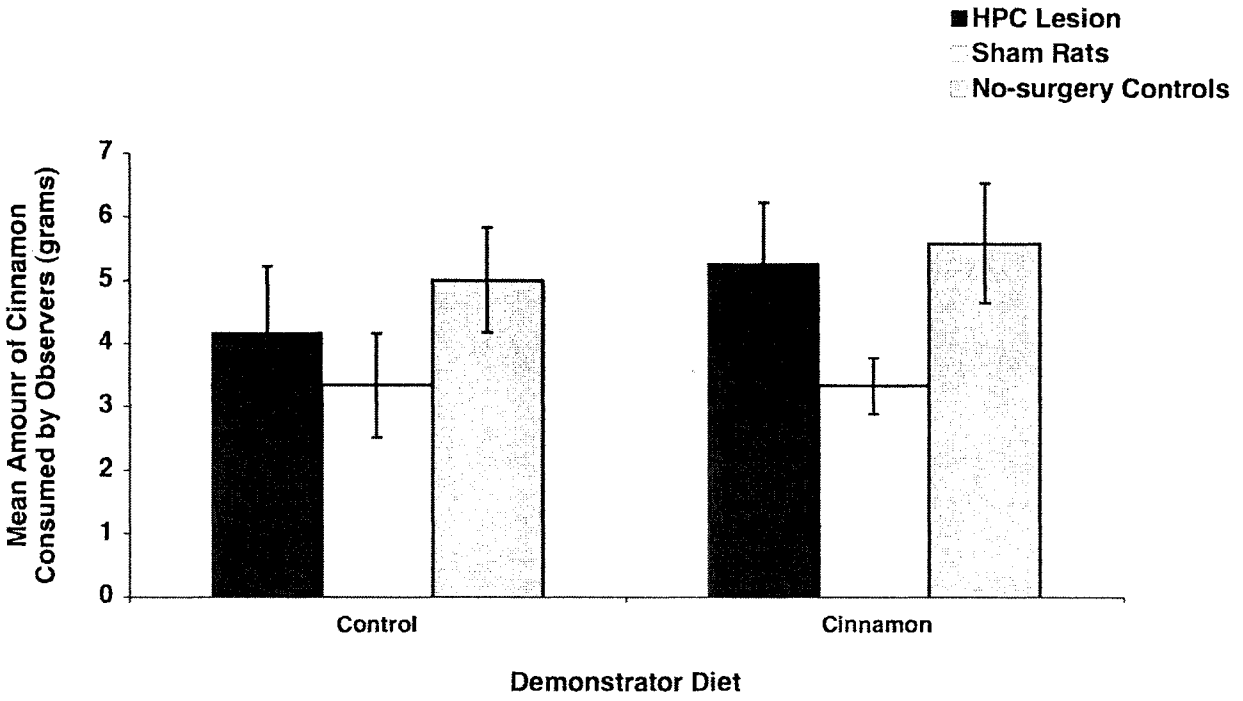

Figure 21. The mean amount of Cinnamon diet consumed by sham-lesion, hippocampal-lesion and no-surgery control Observers during the preference test, following exposure to a Control or Cinnamon Demonstrator. Observers tested under group-learning protocol with a 10 min retention following the learning phase. Error bars represent standard errors of means.

lesion rats ($p > 0.05$) or between sham-lesion rats and no-surgery controls. However, the analysis did reveal a significant difference between the amount of time hippocampal-lesion rats spent interacting with Demonstrator rats ($M = 87.69$, $SD = 63.06$) relative to no-surgery controls ($M = 26.42$, $SD = 23.99$, $p > .05$) (Figure 22).

Figure 23 depicts the fluctuations in interaction over time (30 min session divided into six, 5 min bins) as a function of Experimental Group (Control Demonstrator versus Cinnamon Demonstrator) and Lesion (Hippocampal versus Sham). A 2 X 2 X 6 mixed-factorial ANOVA with Time as the within-subjects factor revealed non significant main effects of Experimental Group ($F(1, 16) = .538$, $p > .05$) and Lesion ($F(1, 16) = 2.84$, $p > .05$) and a non significant interaction between Lesion and Experimental Group ($F(1, 16) = .092$, $p > .05$).

Correlational analyses

Correlational analyses were performed to assess the relationship between Interaction Time (the amount of time Observer rats spent interacting with Cinnamon Demonstrators) and the proportion of cinnamon consumed by sham-lesion and hippocampal-lesion Observers during the test phase. Lesion types were assessed separately. The results of the analysis revealed a significant Pearson correlation between variables in the hippocampal-lesion group (Observers exposed to a Cinnamon Demonstrator) $r(3) = .938$, $p < .05$, $R^2 = .88$) and a non significant Pearson correlation between variables for sham-lesion rats (Observers exposed to a Cinnamon Demonstrator) $r(3) = -.370$, $p > .05$). These data are depicted in Figures 24 and 25. No relationship was found between the proportion of cinnamon consumed and the amount of time

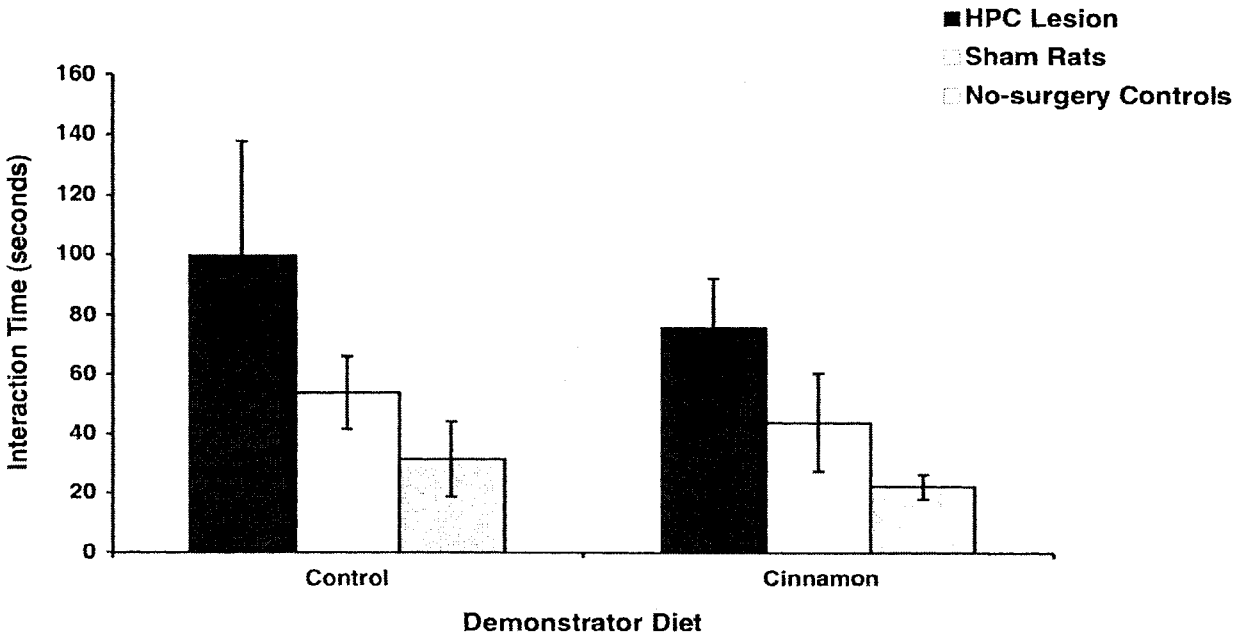

Figure 22. The mean amount of time hippocampal-lesion, sham-lesion or no-surgery Control Observers spent in snout-to-snout contact with Control or Cinnamon Demonstrator rats during the learning phase. Observers were tested under group-learning protocol. Error bars represent standard errors of means.

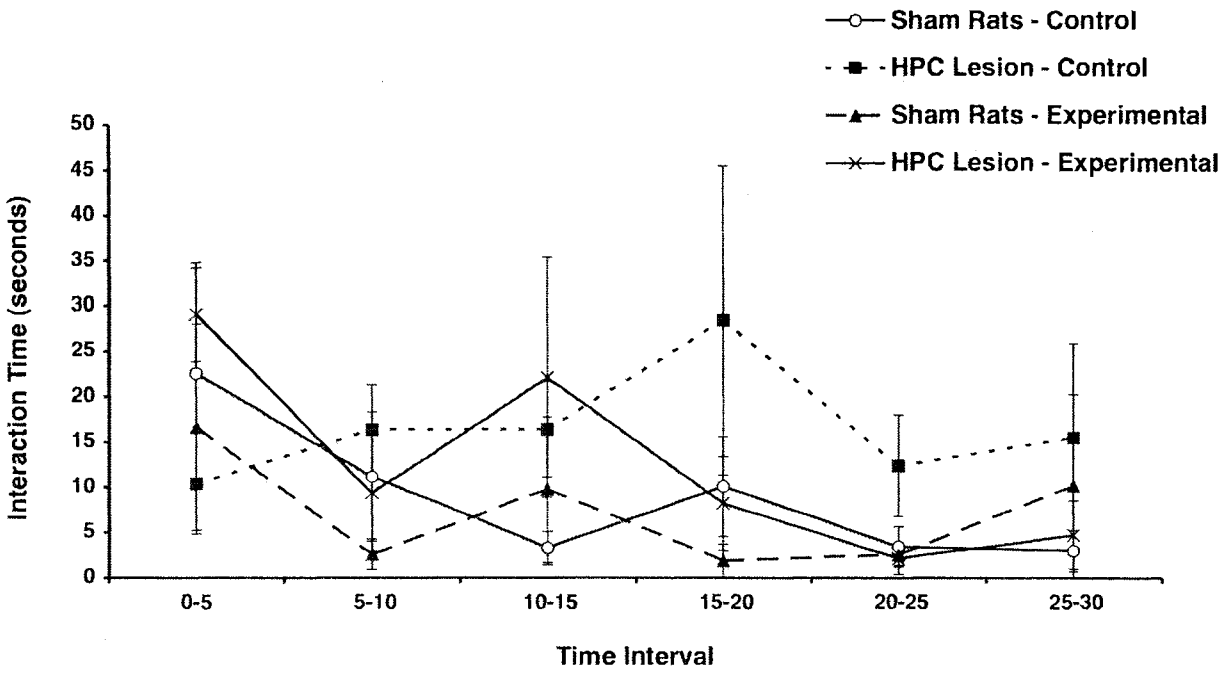

Figure 23. The mean amount of time sham and hippocampal-lesion Observers spent in snout-to-snout contact with Control, or Chocolate and Cinnamon Demonstrator rats during 30 minutes of interaction. Interaction times are divided into 5 min intervals. Error bars represent standard errors of means.

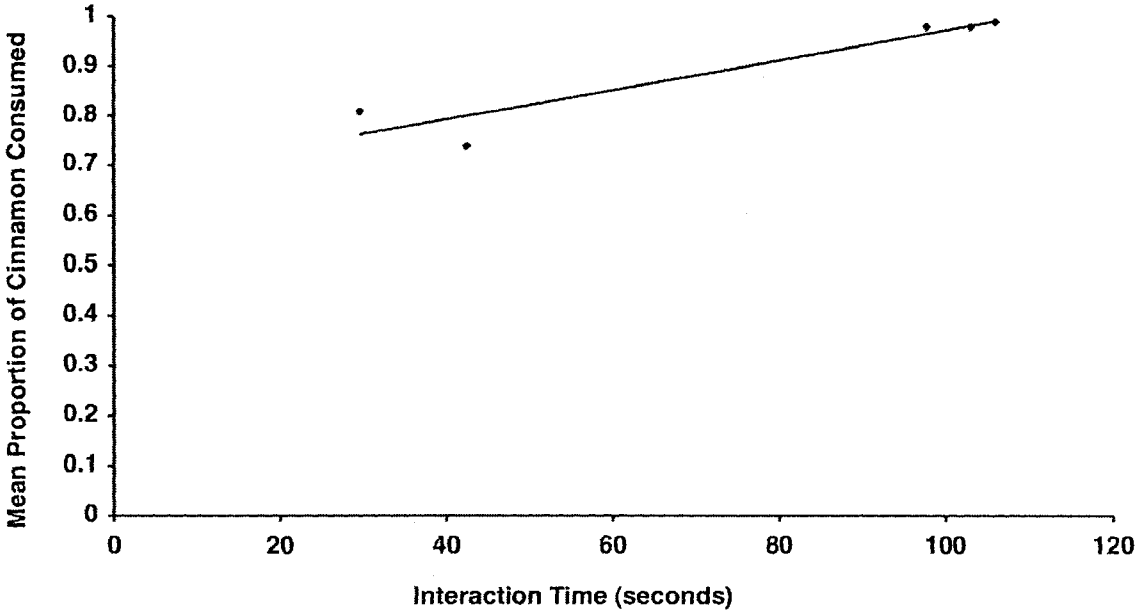

Figure 24. Correlation between the amount of time hippocampal-lesion Observers spent in snout-to-snout contact with Cinnamon Demonstrators and the proportion of cinnamon consumed during the preference test.

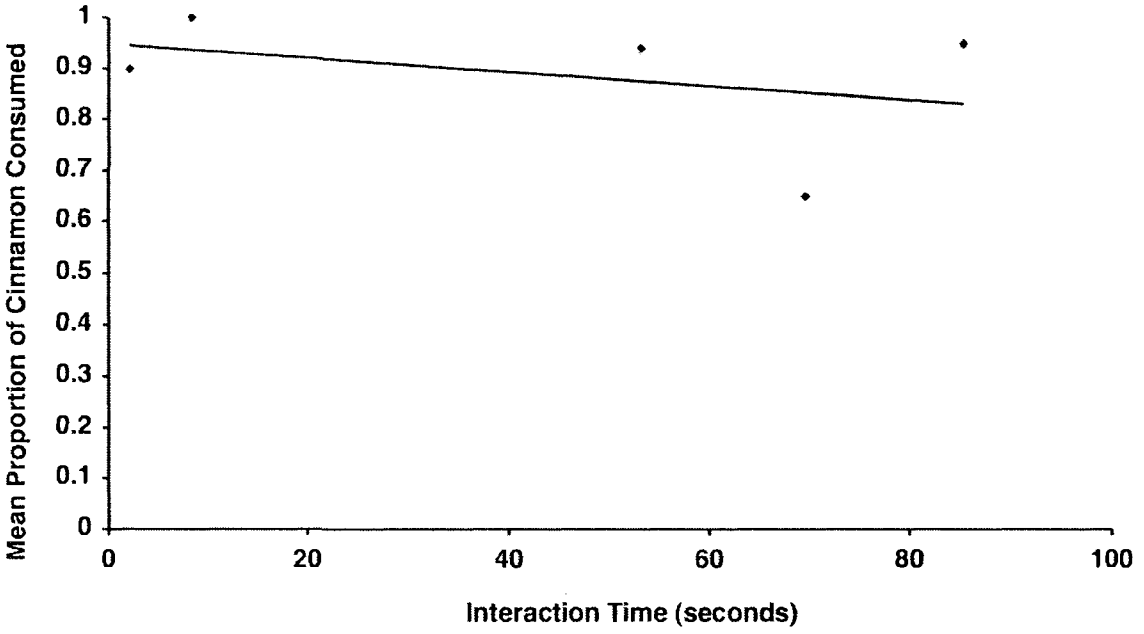

Figure 25. Correlation between the amount of time sham-operated Observers spent in snout-to-snout contact with Cinnamon Demonstrators and the proportion of cinnamon consumed during the preference test.

hippocampal-lesion Observer rats spent interacting with Control Demonstrators ($r(3) = -.240, p > .05$).

DISCUSSION

Following exposure to a Cinnamon Demonstrator rat, hippocampal-lesion and sham-lesion rats ate significantly more cinnamon flavored lard than chocolate flavored lard. Furthermore, hippocampal-lesion rats did not differ significantly from sham-lesion rats exposed to a Cinnamon Demonstrator. Neither group differed significantly from hippocampal-lesion and sham-lesion rats exposed to a Control Demonstrator. However, it should be noted that following exposure to a Cinnamon Demonstrator rats increased their consumption of cinnamon relative to the control group. Collectively, these data suggest that lesions of the hippocampal formation do not disrupt the acquisition or expression of a food preference when the test phase occurs shortly after the learning phase. Furthermore, histological analysis confirmed extensive damage to the hippocampal formation and subiculum, (the type and extent of damage found to produce impairments in the literature using similar lesion techniques (Alvarez, Lipton, Melrose and Eichenbaum, 2001), suggesting that the lack of an impairment in hippocampal-lesion animals is unlikely due to insufficient hippocampal damage and a sparing of hippocampal function.

Close inspection of the data reveal that control animals in Experiment 2 exhibit a preference for cinnamon diet over chocolate. As a result, one could conclude that the effect in the experimental group is attributable not to social learning but rather to a substantial preference in this cohort of subjects for cinnamon flavored foods. However, it should be noted that the magnitude of the preference for cinnamon exhibited by sham and

hippocampal-lesion subjects exposed to a Cinnamon Demonstrator is numerically greater than that exhibited by rats exposed to a Control Demonstrator (88% - 90% versus 77% - 81%; respectively) and exceeds the test-matched preference of Observers exposed to a Cinnamon Demonstrator in Experiment 1A (75%). In no other experiment in this thesis are food preferences induced via exposure to a conspecific equal in magnitude to that seen in the experimental condition of Experiment 2. The robustness of the preference seen in this group suggests that, even if rats from this cohort tended to prefer cinnamon at the outset, an effect of Demonstrator likely occurred and that a ceiling effect is responsible for the lack of a significant difference between the control and experimental animals.

Contrary to Experiment 1A, the amount of time hippocampal-lesion, but not sham-lesion rats, spent interacting with Cinnamon Demonstrators was found to be a significant predictor of later food preferences. As well, hippocampal-lesion rats tended to spend a greater amount of time in contact with Cinnamon and Control Demonstrators relative to sham-lesion and no-surgery controls.

GENERAL DISCUSSION

The main objective of the experiments reported in this thesis was to test the general hypothesis that by fine-tuning test environments to better match the conditions that would support a naturally occurring learning phenomenon, social learning in the laboratory would be enhanced. To test this hypothesis, the ability for rats to acquire a food preference following exposure to a recently fed conspecific was assessed under *conventional-learning* or *group-learning* protocol.

The results of Experiment 1A provide evidence that multiple Observer rats interacting simultaneously with a single Demonstrator (group-learning approach) can acquire a food preference, which persists for a period of at least 24 hr. These results add support to the work of Valsecchi et al. (1996) who suggested that multiple mice living in semi-natural outdoor enclosures acquire, via social transmission, preferences for foods smelled on the breath of Demonstrator mice. The results of Experiment 2 demonstrated that rats with hippocampal-lesions tested under the group-learning protocol acquired a food preference that was evident when the test and learning phases were separated by a 10 min interval. This finding supports previous data on the effects of hippocampal-lesions on the acquisition of a food preference at short intervals (Bunsey et al., 1995; Clark et al., 2002), suggesting that similar underlying neural processes support performance under group and conventional-learning protocol. Overall, the findings from Experiments 1 and 2 lend support to the claims that STFP is a capacity that plays a critical role in guiding the feeding behavior of feral rats.

A main finding of Experiment 1A was that rats tested under conventional protocol did not display as robust a food preference as rats tested under group-learning procedures. Furthermore, the results of Experiment 1B provide preliminary evidence for an interaction between rearing conditions (enriched versus impoverished conditions) and the ability to acquire a food preference under conventional or group-learning protocol. Collectively, these findings suggest that factors other than the joint influences of CS_2 in conjunction with a distinctly scented food are capable of modulating the social transmission of food preferences in domestic rats.

In Experiment 1A, Observer rats were assigned to one of two learning conditions that differed from one another on two counts. In the group-learning condition, the learning phase occurred in the presence of multiple other observers, in the same environmental context as rearing had occurred. Conversely, rats learning under conventional protocol interacted individually with their respective Demonstrators in a context very different from the one they had been reared in. Therefore, one possible explanation for the performance failure of rats learning under conventional protocol relative to rats learning under group protocol may be a mismatch between the cues or releasing stimuli that acquired salience during rearing and the types of stimuli present during learning. The principles of conditioning as well as the behavior systems approach developed by Timberlake (1984) may provide a useful framework within which this interpretation can be understood.

The idea that certain stimuli can act as 'releasers' of conditioned or unconditioned responses forms the basis of the behavior systems approach (Timberlake, 1984). According to Timberlake, behavior is organized within relatively independent systems, each controlling a category of biologically significant behaviors. For example, a rat must perform many activities to survive including obtaining food, finding a mate, avoiding predators etc. Each of these activities is thought to represent a separate behavior system each of which can be elicited by the presence of natural releasing stimuli. Figure 26 depicts the feeding behavior system of a rat. Depending on the stimuli present and the motivational state of the animals, a number of potential responses may be primed or activated. In the case of the hungry rat, the presence of another rat or some other environmental cue may be sufficient to trigger a variety of motor responses geared

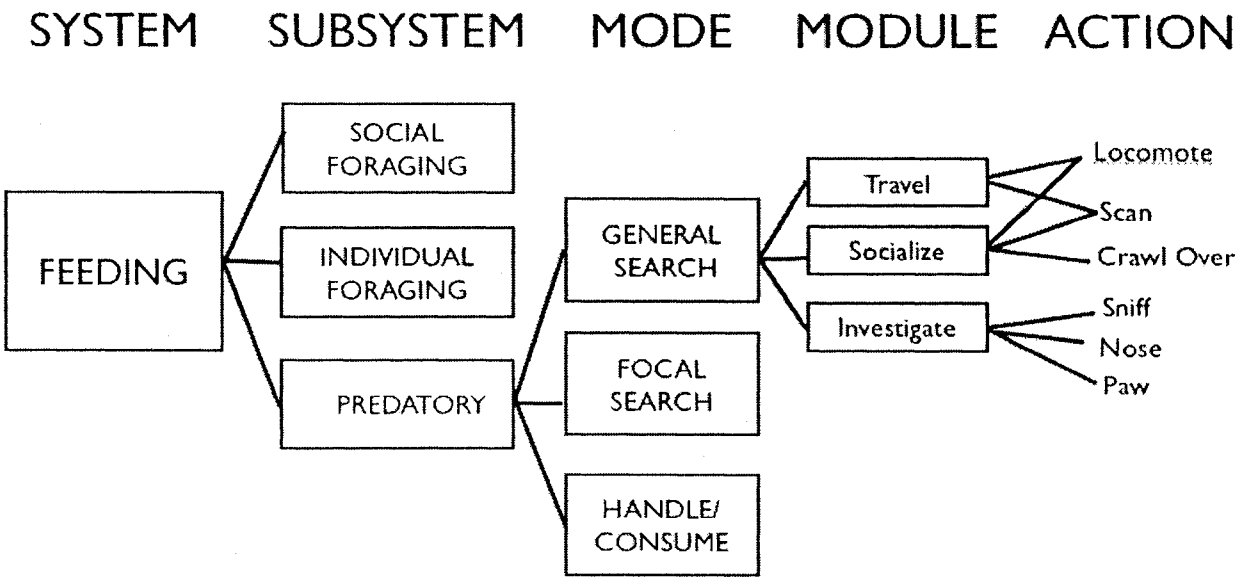

Figure 26. The motivational modes and perceptual-motor modules of the predatory subsystem of the rat's feeding system. (Reproduced from " Motivationl Modes in Behavior Systems", by W. Timberlake, 2000, In: R.R. Mowrer & S.B. Klein (Eds.), *Handbook of Contemporary Learning Theories*, pp. 157. Hillsdale, NJ: Erlbaum Associates).

towards food acquisition (e.g. general or focal search for, or the handling and consumption of foodstuffs).

The kinds of stimuli that will come to act as releasers for particular behaviors will be dictated in large part by the ecological niche of an organism. In the wild, rats likely experience the scent of CS_2 and the smell of flavored foods within a particular context made up of the sounds, sights and smells that characterize their environment. This constellation of stimuli may represent the complete set of triggers necessary to engage the appropriate system and motor responses involved in the search and consumption of foods other colony members are eating. As such, it is conceivable that the failure for rats, raised in enriched conditions but tested under conventional protocol, to display a food preference is due to a mismatch between the kinds of releasers that would have acquired salience during rearing and those present during the learning phase of the experiment. When test conditions during learning were more similar to rearing conditions, as in group-learners, rats readily acquired a food preference. When raised under impoverished housing conditions and tested under conventional protocol (Experiment 1B), rats also acquired a food preference. How might this mismatch affect the acquisition and expression of a food preference? The phenomenon of occasion setting may provide an explanation. Occasion setters are stimuli that come to facilitate or modulate the association between a CS and US, but do not become directly associated with the US themselves. For example, Rescorla (1985) trained pigeons that a 5-second key light was followed by food when the light was preceded by a noise, but not when it was presented alone. The pigeons learned to respond to the lit key at a much higher rate when the noise 'set the occasion' for when the light would be followed by food. In the absence of the

noise responding did occur, but the light appeared to be less effective (Liberman, 2000, p.158). To understand how occasion setting might influence the acquisition and expression of a food preference, it is useful to conceptualize STFP in Pavlovian Conditioning terms. STFP is thought to be mediated by the formation of a stimulus-stimulus association whereby, a rat, following exposure to CS_2 (an unconditioned stimulus) in conjunction with a food cue (a conditioned stimulus), will, upon subsequent exposure to that same food cue, respond by consuming more of it over an equally palatable alternative (conditioned response) (Heyes & Durlach, 1990). In the case of Experiment 1, the stimuli that acquired salience during rearing (through association with foraging episodes and feeding) may 'set the occasion' for learning when present (facilitating the transmission of excitation between CS and US, strengthening the association) and reduce the effectiveness of the CS when absent during learning (as in rats learning under conventional-protocol).

Alternately, the differential between-groups performance of subjects from Experiment 1 may be attributable to systematic differences in satiety between rats tested under conventional and group-learning protocol (e.g. rats learning under conventional-protocol were always sated while rats learning under group protocol always hungry). For example, in the wild, a rat may acquire, encode and store information about what others in the colony are eating but may only be motivated to act on that information at a later time, during a subsequent foraging bout. If hunger levels did differ between groups, one might expect to see differences in the total grams of food consumed during the preference test between the group and conventional-learning conditions. No such effect was found.

A secondary finding from Experiment 1 was the failure to detect a correlation between the amount of time spent in snout-to-snout contact with Demonstrator rats and the magnitude of acquired food preferences. Furthermore, Observers learning under conventional protocol spent consistently more time interacting with Demonstrator rats relative to Observers in the group-learning condition, yet failed to display a food preference. Although work by Galef & Stein (1985) has shown that investigation of the anterior end of live Demonstrator rats by Observers is key for the successful transmission of food preferences (however Observer rats separated from Demonstrator rats by a screen mesh and denied physical contact will acquire a preference), these data suggest that exposure alone and not the amount of exposure to the appropriate cues is important.

The comparatively low investigation times found among group-learners as compared to rats learning under conventional protocol may be thought of as providing further evidence for 'enhanced learning' under group-protocol. For example, it could be said that rats learning under group protocol required less exposure time to successfully acquire a food preference in comparison to rats learning under conventional protocol. However, differences in the amount of space and learning opportunities available to Observers tested under group-learning versus conventional learning protocol may account for the discrepancy in interaction times. For example, the use of large complex environments may have resulted in less redundant exploration of Demonstrator rats by Observers simply by virtue of the greater space availability in one learning condition over another. Alternately, the presence of multiple Observers competing for interaction time with a single Demonstrator may have reduced the amount of overall opportunities for interaction between Observer and Demonstrator rats tested under the group protocol.

Another trend evident in the interaction data is that Observers from both the conventional and group-learning conditions spent a consistent amount of time across the 30 min session interacting with Demonstrator rats. Interestingly, neither group differed in comparison to their respective control groups. The fact that Observers (in both group and conventional-learning conditions) spent similar amounts of time with control and experimental Demonstrators suggests that interactions were neither maintained nor elicited by the odor of a novel foodstuff on the breath of Demonstrator rats. Were the opposite to be true, one might expect to see an initial eagerness on the part of Observers to interact with both control and experimental Demonstrators, accompanied by a more rapid drop in interest over time in the control group relative to the experimental groups (it is possible that such a trend would have become apparent were the interaction phase have been longer). The lack of such a differential effect suggests that the mechanism underlying the social transfer of information is an innate behavioral tendency for rats to approach, sniff, greet and interact with other members of the species, thereby providing the indirect means by which learning about the foods others are eating can incidentally occur. Based on this hypothesis, one could predict that if the amount of time any two Observers in the group-learning condition spent in interaction with one another were measured, interaction times would not differ significantly from those obtained for Demonstrator/Observer instances of interaction.

Following a 10 min retention interval, hippocampal-lesion rats from Experiment 2 display a tendency to select for consumption the diet smelled in association with their Demonstrator rat. These findings are consistent with data from lesion experiments

demonstrating spared anterograde memory for socially learned information when the test and learning phase are separated by short intervals (Bunsey & Eichenbaum, 1995).

This finding suggests that other structures are involved in the processing of STFP and capable of supporting performance when the learning and test phase are separated by short delays (10 min). Research by Wang, Fontanini & Katz (2006) found evidence that the amygdala plays an important role in STFP. In their study, rats were tested with either an intact amgydala or following temporary inactivation of the amygdala with muscimol during training. Impairments were observed when the test phase occurred at both 1 day and 7 days following the learning phase. Furthermore, subjects infused with the anesthetic drug during the testing phase performed normally in comparison to subjects that received similar infusions at the time of learning ruling out non-specific drug effects as the basis for impairments. The role of the basolateral amygdala in STFP should come as no surprise. This structure receives direct projections from the olfactory piriform cortex, the parabrachial nuclei and insular cortex (involved in the processing of gustatory and olfactory information).

The interaction data from Experiment 2 showed that overall, hippocampal-lesion rats tended to spend more time with Demonstrator rats than sham-lesion animals, and the amount of exposure to food cues on the breath of Demonstrator rats was positively correlated with the expression of a food preference. Although Experiment 2 provides evidence suggesting that the hippocampus is not necessary for the acquisition or expression of a food preference when the learning and test phase are separated by a 10 min interval, the behavioral data suggests that rats without a hippocampus are more reliant on a particular element of the learning phase; the amount of exposure to the food

cue. It may be that the performance of hippocampal-lesion rats reflects the operation of non-associative processes, rather than the stimulus-stimulus association thought to underlie performance in intact animals (Bunsey et al., 1995, Alvarez et al., 2001). For example, a reduction in the neo-phobic response towards the more familiar of the two diets as a function of exposure time (Clark et al., 2002).

The findings from Experiment 2 provide some support for common neural systems supporting performance using group and conventional learning procedures, however this evidence is preliminary. Future studies should aim to assess the role of the hippocampus in the retrograde direction across several different time points (memory for preferences acquired at various time points prior to hippocampal damage) as well as the effects of hippocampal lesions on the ability for rats to acquire and express a food preference at long delays between acquisition and the test phase (e.g. following a 24 hr interval).

The general aim of this thesis was to assess whether the learning of food preferences in laboratory rats would be enhanced under semi-natural conditions. In order to test this hypothesis, modifications were made to the conventional paradigm used to study STFP so as to capture the social dynamic that would likely underlie learning in a rat's natural habitat. This created a unique opportunity to test the reliability of a new technique for the study of STFP in laboratory rats. Rather than the one-to-one demonstrator to observer interaction ratio used in the conventional paradigm, the group-learning approach uses a multiple-observer to single demonstrator interaction ratio. The findings from Experiment 1A validate the utility of the group-learning approach and provide evidence for an efficient and cost effective alternative for the study of STFP in laboratory rats. Furthermore, taken together with previous work demonstrating the robustness of socially

transmitted food preferences (Clark et al., 2002; Galef et al., 1984; Galef et al., 1998, Galef et al., 2005, Galef & Whiskin, 1992, Galef et al., 1990, Galef and Kennett, 1985), the finding that groups of observer rats interacting simultaneously can acquire a food preference adds support to the claim that STFP functions in information transfer in natural settings. Additionally, behavioral data from the interaction phase of Experiment 1 suggest the mechanism supporting the transfer of information between Observer and Demonstrator is passive in nature and motivated by an innate tendency for rats to approach and investigate one another.

The data from this thesis generate several potential directions for future research. The findings from Experiment 1 suggest that a mismatch between the rearing and learning context explain the performance failures of rats tested under conventional protocol, however they do not provide insight into which of the constellation of stimuli present during rearing became critical in mediating the learning and expression of a food preference. For example, the features that comprise the environmental context itself or the presence of multiple other conspecifics during rearing or both of these elements combined may have acquired occasion setting abilities. A first step towards delineating this critical element might involve comparing the magnitude of learning when a *single* Observer (conventional protocol) or *multiple* Observers (group-learning approach) are exposed to a Demonstrator rat within the large complex environments used during rearing.

Furthermore, although rats interacting under group protocol in Experiment 1A did acquire a food preference that was greater in magnitude than that acquired by rats learning under conventional protocol, evidence for enhanced learning may be manifest

along other dimensions. For example, Observers learning under group protocol may require less time overall to acquire a food preference than rats learning under conventional protocol, and food preferences learned this way may be found to persist for longer time intervals than previously found in the literature (Galef & Whiskin, 2001, Clark et al., 2002).

In sum, the main findings of this thesis were: 1) multiple observer rats interacting simultaneously with a single demonstrator rat can acquire a food preference evident up to 24 hr following the learning phase; 2) rats learning under group-protocol acquired a more robust preference than rats learning under conventional-protocol; 3) evidence for an interaction between rearing conditions and the performance of Observer rats as a function of learning condition; 4) the amount of exposure to food cues on the breath of Demonstrator rats is not correlated with later food preferences in intact animals and 5) hippocampal lesions do not disrupt the acquisition and expression of a food preference when the test and learning phase are separated by a 10 min interval.

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APPENDIX A

Stereotaxic coordinates for the HPC lesions

Table A1

The cannulae coordinates, in mm relative to bregma, for the neurotoxic lesions of the HPC.

Anteriorposterior (AP)	Mediolateral (ML)	Dorsoventricular (DV)
3.1	1.5	3.6
4.1	2.8	4
5	3	4.5
5.3	5.2	7
6	5	7.3